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Frasnian (Upper Devonian) rugose corals from
the Lime Creek and Shell Rock Formations of Iowa

by

James E. Sorauf

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CONTENTS

	Page
Abstract	7
Introduction	7
Acknowledgments	8
Stratigraphy	9
Shell Rock Formation	9
Mason City Member	9
Rock Grove Member	10
Nora Member	12
Lime Creek Formation	14
Cerro Gordo Member	14
Owen Member	17
Biostratigraphy	21
Field Conditions	23
Systematic Paleontology	24
Introduction	24
Repositories	25
Systematics	27
Family Endophyllidae	27
Genus <i>Iowaphyllum</i>	28
<i>I. johanni</i>	31
Family Kyphophyllidae	33
Genus <i>Tabulophyllum</i>	33
<i>T. rectum</i>	34
<i>T. ehlersi</i>	35
<i>T. rotundum</i>	36
<i>T. ellipticum</i>	37
<i>T. ponderosum</i>	38
<i>T. robustum</i>	39
<i>T. longum</i>	39
<i>T. magnum</i>	41
<i>T. expansum</i>	43
<i>T. mutabile</i>	44
<i>T. curtum</i>	45
<i>T. levorsoni</i>	46
<i>T. buccinum</i>	47
<i>T. sp. A</i>	48
<i>T. sp. B</i>	48
Genus <i>Tarphyphyllum</i>	49
<i>T. cylindricum</i>	49
<i>T. sp. A</i>	50
Genus <i>Smithiphyllum</i>	51
<i>S. belanskii</i>	51
Family Charactophyllidae	53
Genus <i>Charactophyllum</i>	53
<i>C. nanum</i>	54
Family Disphyllidae	57
Genus <i>Disphyllum</i>	57
<i>D. dispassum</i>	58
<i>D. floydense</i>	59
<i>D. conjugans</i>	61
<i>D. iowensis</i>	62
Genus <i>Hexagonaria</i>	63
<i>H. bassleri</i>	64
<i>H. bassleri bassleri</i>	66
<i>H. bassleri magna</i>	67
<i>H. oweni</i>	67
<i>H. inequalis</i>	68
Family Phillipsastreidae	70
Genus <i>Pachyphyllum</i>	70
<i>P. minutissimum</i>	73

<i>P. gregarium</i>	75
<i>P. websteri</i>	76
<i>P. woodmani</i>	78
<i>P. crassicostatum</i>	80
<i>P. dumonti</i>	82
Genus <i>Trapezophyllum</i>	84
<i>T. sp. A</i>	84
Genus <i>Macgeea</i>	85
<i>M. solitaria</i>	86
<i>M. camplanulata</i>	89
<i>M. concinnula</i>	90
References Cited	91
Appendix—Fossil Localities	96
Plates	100
Index	157

LIST OF ILLUSTRATIONS

Text-figure	Page
1. Index map of outcrop area of Frasnian strata in north-central Iowa.	10
2. Composite stratigraphic section of the Shell Rock Formation as it is exposed along the Shell Rock River.	11
3. Outcrops of Mason City Member at its type locality.	12
4. The Shell Rock Formation exposures in the region between Nora Springs and Rockford, Iowa.	13
5. Exposures of the uppermost carbonates of the Mason City Member along the Shell Rock River just downstream of the Nora Dam.	14
6. Shell Rock Formation on east wall of Tom Williams Quarry.	15
7. North to south cross section of the Mason City Member of the Shell Rock Formation between Nora Springs and Greene (Marble Rock Quarry) and Roseville, Iowa.	15
8. Exposures of the entire Mason City Member at Cooper's Bend.	16
9. Exposures of the Shell Rock Formation along the Shell Rock River northwest of Greene, Iowa.	16
10. Closeup of large stromatoporoid in lower Nora biostrome.	17
11. Localities where the Shell Rock Formation was studied along the Shell Rock River northwest of Nora Springs, Iowa.	18
12. Stratigraphic section illustrating changes in the Nora Member in a northwest to southeast traverse along the Shell Rock River north of Nora Springs, Iowa.	19
13. Nora Member at Weitsie's Bluffs.	19
14. Two stratigraphic sections of the Nora Member.	20
15. Location of exposure of Nora Member at Rudd, Iowa.	20
16. Outcrop localities of the Lime Creek and Shell Rock Formations along the Winnebago River and its tributaries.	21
17. Outcrops of the Lime Creek Formation.	22
18. Photograph to illustrate changing quality of the outcrop of the upper part of the Cerro Gordo Member of the Lime Creek Formation at Bird Hill. Photo taken August, 1967.	23
19. Photograph to illustrate changing quality of the outcrop of the upper part of the Cerro Gordo Member of the Lime Creek Formation at Bird Hill. Photo taken June, 1986.	23
20. Composite stratigraphic section of the Lime Creek Formation.	24
21. Photograph taken in 1968 illustrating the method of digging clay at the Rockford Brick and Tile Company Quarry.	25
22. Photograph taken in 1968 illustrating the method of digging clay at the Rockford Brick and Tile Company Quarry. Weathered face of lower Cerro Gordo Member.	25
23. Correlation of the Cerro Gordo Member strata west to east.	26
24. Stratigraphic section showing correlation of beds within the Owen Member.	26
25. Exposures of the Owen Member of the Lime Creek Formation in the Rockwell area, north of Sheffield, Iowa.	27
26. Location of three quarries in the Owen Member, located due south of Dumont, in Butler County, Iowa.	27
27. Upper part of the Owen Member of the Lime Creek Formation at Carrolus Quarry, 1968.	28
28. Complete sequence of the Owen Member of the Lime Creek Formation at the Buseman Quarry, south of Dumont, Iowa.	28
29. Location of the Morgan Quarry (Owen Member).	29
30. <i>Iowaphyllum johanni</i> , from the Cerro Gordo Member, colony mean diameters (in mm) vs. colony mean number of total septa.	32
31. Corallite diameter vs. total number of septa in each corallite for <i>Tabulophyllum longum</i> , <i>Tabulophyllum magnum</i> , and <i>Tabulophyllum expansum</i>	40
32. Corallite diameter (in mm) vs. number of major septa in <i>Tabulophyllum mutabile</i> n. sp.	44
33. Corallite diameter (in mm) vs. the total number of septa in <i>Tabulophyllum curtum</i> n. sp.	46
34. Corallite diameters (in mm) vs. number of major septa in each corallite in <i>Tarphyphyllum cylindricum</i> n. sp.	50
35. Corallite diameter (in mm) vs. number of total septa for individual corallites in <i>Smithiphyllum belanskii</i>	52
36. Corallite diameter (in mm) vs. number of major septa for individuals in <i>Charactophyllum nanum</i>	55
37. Corallite diameter (in mm) vs. total number of septa in individuals in <i>Disphyllum dispassum</i>	59

38. Colony mean diameter of tabularium (in mm) vs. colony mean number of total septa in <i>Disphyllum floydense</i>	60
39. Colony mean diameter of tabularium (in mm) vs. colony mean for total number of septa in <i>Hexagonaria bassleri</i>	65
40. Colony mean diameter of tabularium (in mm) vs. colony mean for total number of septa in each corallite in <i>Hexagonaria oweni</i>	67
41. Colony mean diameter of tabularium (in mm) vs. colony mean for total number of septa in each corallite in <i>Hexagonaria inequalis</i>	69
42. Colony mean diameter of tabularium (in mm) vs. colony mean number of total septa in <i>Pachyphyllum minutissimum</i> and <i>Pachyphyllum gregarium</i>	73
43. Colony mean diameter of tabularium (in mm) vs. colony mean number of total septa in each corallite in <i>Pachyphyllum websteri</i>	76
44. Colony mean diameter of tabularium (in mm) vs. colony mean number for total number of septa in corallites in <i>Pachyphyllum woodmani</i>	79
45. Colony mean diameter of tabularium (in mm) versus colony mean for total number of septa in corallites in <i>Pachyphyllum crassitcostata</i>	81
46. Colony mean diameter of tabularium (in mm) vs. colony mean for total number of septa in corallites in <i>Phillipsastrea dumonti</i> n. sp.	82
47. Diameter of corallite (in mm) vs. total number of septa in <i>Macgeea solitaria</i>	87
48. Diameter of corallite (in mm) vs. total number of septa in <i>Macgeea concinnula</i> n. sp.	89

LIST OF TABLES

Table	Page
1. Stratigraphic subdivisions of outcropping units of the Shellrock Formation, as slightly modified from Belanski (1927).	11
2. Stratigraphic distribution of species of rugose corals within the Shell Rock and Lime Creek Formations of north central Iowa.	29

FRASNIAN (UPPER DEVONIAN) RUGOSE CORALS FROM THE LIME CREEK AND SHELL ROCK FORMATIONS OF IOWA

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ABSTRACT

Rugose corals from Frasnian Lime Creek ("Hackberry") and Shell Rock strata are known largely from the works of Fenton and Fenton (1924) and Belanski (1927, 1928), each of which described outcrop stratigraphy and major parts of the fauna. The Shell Rock Formation includes three members, two of which contain rugosans, the basal Mason City and the uppermost, or Nora Member. The overlying Lime Creek Formation contains the Juniper Hill Member, lacking corals, overlain by the very fossiliferous Cerro Gordo Member, source of much of the famous "Hackberry" coral fauna described by Fenton and Fenton in 1924. The uppermost, Owen Member, also contains abundant Rugosa.

Considerable diversity is present in these Frasnian corals. The Family Endophyllidae is represented by *Iowaphyllum johanni*. Kyphophyllidae include the genera *Tabulophyllum*, *Tarphyphyllum*, and *Smithiphyllum*. Species of *Tabulophyllum* are especially abundant in both the Lime Creek and Shell Rock faunas. The type species, *T. rectum*, occurs only within the Cerro Gordo Member, with its synonyms, *T. regulare* and *T. erraticum*. Cerro Gordo beds also contain a small ovate form, *T. ehlersi* and the more robust *T. rotundum*, each greatly resembling *T. rectum* as juveniles. The Cerro Gordo also contains the larger species *Tabulophyllum robustum*, a large ovate form, *T. ellipticum*, and additionally, the largest of the Cerro Gordo solitary corals, *T. ponderosum*. The overlying Owen Member contains large *Tabulophyllum* species, with *T. longum*, the most numerous, *T. magnum*, often bilaterally symmetrical, and *T. expansum* the largest of the solitary Lime Creek species.

Tabulophyllum also abounds in Shell Rock beds; *T. mutabile* n. sp. occurs in the Mason City, with uppermost beds of this unit also characterized by *Tabulophyllum curtum* n. sp. The Nora Member has stromatoporoid biostromes which contain the robust species *T. buccinum* n. sp. and large specimens of *T. levorsoni* n. sp.

The kyphophyllid *Tarphyphyllum cylindricum* n. sp. is common in the lower Nora Member, and a single specimen of a second, unnamed new species of this genus is also present in the same unit. The most common kyphophyllid of the Shell Rock is the branching colonial species *Smithiphyllum belanskii*, characteristic of the lower Mason City biostrome.

The Cerro Gordo contains the type species of the Charactophyllidae, *Charactophyllum nanum*, a solitary, non-carinate coral with denticulate septa and thick, feathery septal trabeculae. This is the most abundant coral of the Lime Creek. The Disphyllidae are abundantly represented in the Iowa faunas by species of *Disphyllum* and *Hexagonaria*. *Disphyllum dispasum* is present in the Cerro Gordo, while underlying Shell Rock beds have numerous *Disphyllum floydense* in the uppermost beds of the Mason City, accompanied by *D. iowensis* n. sp. The Nora species, *Disphyllum conjugans* n. sp., is small and along with *Hexagonaria oweni* occurs abundantly within biostromes of the member. The genus *Hexagonaria* is also abundantly represented in the Cerro Gordo fauna by *Hexagonaria inequalis* and in the Owen by *H. bassleri*. There are two subspecies of the latter, *H. bassleri bassleri*, the typical form, and very large diameter corals placed in *H. bassleri magna*.

The Family Phillipsastreidae is present in abundance in both formations. The colonial corals are species of *Pachyphyllum*. From the base, the Shell Rock strata contain *Pachyphyllum minutissimum* and *P. websteri* in the Mason City Member, and *P. gregarium* in the Nora. Lime Creek species are, *P. woodmani* in the Cerro Gordo Member, and *P. crassicosatum* and *P. dumonti* n. sp. in the Owen Member. These species are highly variable, but form characteristic assemblages and are valuable stratigraphic markers within the Iowa sequence. Several species of Webster and Fenton are regarded as synonyms of *Pachyphyllum woodmani*; *P. ordinatum* and *P. levatum*. *Pachyphyllum irregulare* also belongs in *P. woodmani*, although it is at the very large end of size in this species. The upper Owen Member is characterized by *Pachyphyllum crassicosatum*, composed of colonies with large diameter corallites. In the southern area of Owen outcrops, a small-diameter form of the genus, *Pachyphyllum dumonti* n. sp., replaces the large *P. crassicosatum* as the typical Owen form of the genus. Lastly, a single specimen of *Trapezophyllum* sp. was found in the Mason City Member, the first occurrence of this genus in central North America.

Abundant solitary phillipsastroid corals of these faunas are placed in *Macgeea*. The Cerro Gordo characteristically contains the highly variable species, *Macgeea solitaria*, and a neotype is here proposed for the species. The Owen Member contains *M. camplanulata* n. sp., a large species with less variability than *M. solitaria*. Within the Shell Rock, a small diameter species, *Macgeea concinnula* n. sp., is abundant in the Nora Member.

Based on the brachiopod and conodont zonation, the Shell Rock and Lime Creek coral faunas are medial and late, but not latest Frasnian.

INTRODUCTION

Frasnian coral faunas of north-central Iowa are renowned; their scientific importance stems from their

abundance, excellent preservation and occurrence within well-exposed strata. Both the solitary and colonial Rugosa of the older Shell Rock Formation and the younger Lime Creek Formation are treated here.

The younger fauna is that described by C.L. and M.A. Fenton (including work by C.L. Webster) in 1924, in their monograph on the fauna of the "Hackberry Stage of Iowa". By modern standards, the fossil corals were not adequately described by the Fentons, who defined species on few specimens, with too much emphasis on external form and growth characteristics, and with too little attention paid to their occurrence within variable populations. In spite of this, the Lime Creek corals became known to the world, and many paleontologists have either collected topotypic material from Iowa, or studied the abundant material distributed throughout the world. Thus, these corals, with their excellent preservation, have been individually studied by many coral workers, but prior to the 1960's no one undertook the restudy of the entire fauna.

In addition to the widely known coral faunas of the Lime Creek Formation, earlier Frasnian rocks belonging to the Shell Rock Formation occur in the same outcrop area (Text-fig. 1) and are richly fossiliferous, including a varied coral fauna. Published descriptions of several of the Shell Rock corals are those of Charles Belanski (1927, 1928). He began paleontological studies in this unit as a young amateur, collecting in outcrops near his home in Nora Springs, Iowa. Belanski systematically collected from Shell Rock beds, and at the time of his early death, left extensive collections at the University of Iowa, accompanied by detailed stratigraphic and locality data.

Both the Shell Rock and Lime Creek rugose coral faunas are composed of cosmopolitan Frasnian genera, and have species in common with age-equivalent North American faunas in New York, New Mexico, Nevada and western Canada. They also have many genera in common with Frasnian faunas farther afield, in Belgium and northern France, Germany, southern England, Poland, Russia, China and Australia. Thus, the Iowa fauna containing species and genera established by Hall and Whitfield (1873), Webster (1889a,b) and Fenton and Fenton (1924), plays a major role in understanding the morphology, taxonomy and nomenclature of Upper Devonian rugosans. The Lime Creek fauna contains type species of *Charactophyllum* Simpson, 1900, *Tabulophyllum* Fenton and Fenton 1924, *Iowaphyllum* Stumm 1949, and *Macgeea* Webster 1889b. Thus, understanding of Frasnian coral faunas worldwide requires an understanding of the Iowa material. The earlier Frasnian Shell Rock coral fauna is less well-known than that of the Lime Creek, but these corals are also abundant and are more diverse than those of the Lime Creek. The Shell Rock contains species of such important, widely distributed genera as *Smithiphyllum*, *Trapezophyllum*, *Tarphyphyllum* and *Disphyllum*, as well as species of the genera *Macgeea*,

Tabulophyllum and *Pachyphyllum* that occur in both units.

ACKNOWLEDGMENTS

The work involved in this study first began in 1967, with initial field investigations, and has continued intermittently since that time. I am indebted to a number of individuals who have helped me at various stages of the study; they are truly numerous and I cannot here properly thank all of them.

Calvin Levorson, then postmaster of Riceville, Iowa, accompanied me in the field in the late 1960's and early 1970's, and shared with me his encyclopedic knowledge of outcrops and collecting localities, including those of Charles Belanski. Donald L. Koch, then geologist (now Director) of the Iowa Geological Survey, shared his knowledge of the Shell Rock Formation, and Harrell Strimple (deceased) of the University of Iowa aided me in borrowing collections and providing me with locality information regarding the Frasnian faunas of north-central Iowa. Professors William Furnish, Brian Glenister and Gilbert Klapper of the University of Iowa all gave freely of their wisdom and good will. Ms. Julia Golden of the University of Iowa has kindly arranged for loans of specimens from the Belanski Collection. Professor Donald B. Macurda, Jr., then of the University of Michigan, arranged for my borrowing specimens from the Fenton collections at the University of Michigan Museum of Paleontology. Dr. Matthew H. Nitecki and Ms. Phyllis N. Windle aided by arranging for loans of Fenton types from the Field Museum of Natural History. Dr. Bruce Bell made it possible for me to borrow Hall and Whitfield specimens from the New York State Museum of Natural History. Mr. Frederick J. Collier and Mrs. Jann Thompson have been similarly gracious in arranging for loans of Webster types and other specimens at the United States National Museum of Natural History (Smithsonian Institution). At Binghamton University, thin sections of corals have been made with skill by Mr. Frank Sedlak and Mr. Richard Jacyna. Photography has been by Mr. David Tuttle. Ms. Anne D. Hull has prepared all maps and charts for this publication. Dr. Carl W. Stock spent one field season with me in Iowa while he was working on stromatoporoid faunas of the Upper Devonian of Iowa. Professional expertise and criticism of this manuscript have been provided by Dr. William A. Oliver, Jr. of the United States Geological Survey, and by Dr. Ross A. McLean of Amoco Canada Petroleum Co. Ltd. Biostratigraphy has been reviewed by Professor Gilbert Klapper of the University of Iowa.

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STRATIGRAPHY

SHELL ROCK FORMATION

The stratigraphy of the outcropping Shell Rock Formation is based on early work by Belanski (1927, 1928) and a more recent study by Koch (1970). Regional study of the Middle and Upper Devonian rocks of northern Iowa by Witzke and Bunker (1984, 1985, 1996), and by Witzke *et al.* (1989), has greatly clarified our understanding of the east-west facies change in the unit (from the outcrop into the subsurface), providing analyses of regional and sequence stratigraphy, and its tectonic control.

Throughout the study area in north-central Iowa (Text-fig. 1), the Shell Rock Formation is underlain by the Lithograph City Formation of Witzke *et al.* (1989, p. 241). These underlying beds had previously been referred to as "Cedar Valley" in a general sense. Facies and lithic relationships have been given intensive study by the Iowa Geologic Survey, and the Cedar Valley has been redefined as the Cedar Valley Group (Witzke *et al.*, 1989, p. 229), containing the Shell Rock Formation (Text-fig. 2) as well as underlying lowermost Frasnian and Middle Devonian strata.

Table 1 summarizes the subdivisions of the Shell Rock according to Belanski (1927). This division into members is workable and practical in outcrop stratigraphy, as units are here distinctive, although their geographic extent is confined to the Shell Rock River Valley. These outcrops along the Shell Rock River are most important for study of coral faunas, thus, Belanski's stratigraphy remains most useful. Because of facies changes, and accompanying faunal changes, however, the subdivisions Belanski used within the "zones" or beds shown on Table 1 are not useful except as indices to outcrops bearing particular faunal elements. The members are discussed in ascending order.

MASON CITY MEMBER

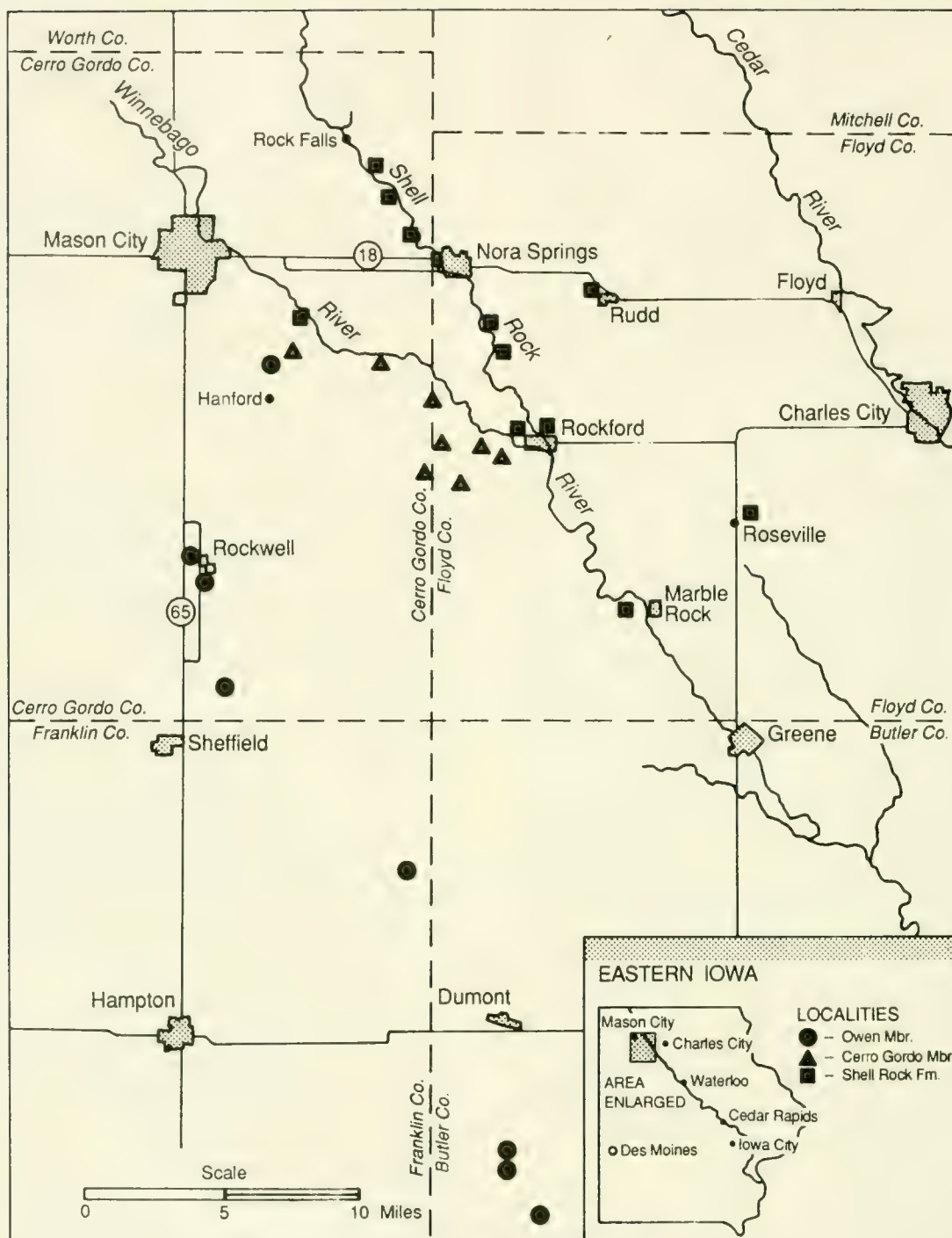
The Mason City Member is 6.9 m thick at its type section (Koch, 1970, p. 63), where mostly thick-bedded limestones form a cliff along the east bank of the Shell Rock River (Text-fig. 2). This cliff (Text-fig. 3) is present for approximately 0.75 mile (1.2 km) along the bank, extending through the center of the SE $\frac{1}{4}$, Sec. 7, T. 96 N., R. 18 W., Floyd County, Iowa (Nora Springs Iowa 7 $\frac{1}{2}$ ' Quadrangle). The type section is located beneath the bridge that bears U.S. Highway 18 west from Nora Springs (Locality 9, Text-fig. 4), so designated by Belanski (for his Mason City Substage

of the Shellrock Stage, 1927, p. 332) and accepted by Koch (1970, p. 9).

The Mason City Member is best exposed along the Shell Rock River, from the north edge of Nora Springs, where the top of the unit is exposed just below the old mill dam (Text-fig. 5), southward towards Rockford in cliffs along the river, and in the low bluffs along the river between the old Baumgardner's Mill Run and Rockford to the south. Outcrops in Nora Springs (locs. 8 and 9, Text-fig. 4) south of Nora Springs (Locality 10) and at Williams Quarry (Locality 16, Text-figs. 4,6) and Baumgardner's Mill (Locality 17) are of thick sequences of Mason City rocks that form considerable cliffs along the river. South of the Baumgardner's Mill locality, outcrops are low along the banks of the river, and only the top beds are exposed, as at Cooper's Bend (Locality 19, Text-figs. 4,8), and at Kapka's Farm, locality 18. Locality names are mostly from Belanski, 1927, to provide continuity to that date, with detailed locations given in the Appendix. In the town of Rockford, most of the Mason City Member is exposed along the Shell Rock River in the east part of the village, but as these are cliff exposures, few fossil corals could be collected and little time was devoted to these outcrops.

Koch provided isopachous maps of the Mason City Member (1970, fig. 4, p. 11) with contours oriented NNW-SSE. The maximum thickness is present near Nora Springs, with thickness trends extending through Rockford, where beds are still in excess of 4.5 m, to the area of Marble Rock (Text-fig. 9), where the member remains approximately 2.5 m thick at Areola (Bunker *et al.* 1986, p. 38). Here, coral faunas are still common in the upper part of the member. The southernmost locality where Mason City coral faunas were encountered was at the Maxson Quarry west of Marble Rock (Text-figs. 1,9) described by Bunker *et al.* (1986, p. 38). Here the lower biostromal beds of the Mason City are exposed on the upper, stripped surface of the quarry, overlying the Lithograph City Formation, also part of the Cedar Valley Group.

The Mason City Member in this outcrop area is largely composed of biostromal limestones above a thin basal dolomite, with biostromes followed by two overlying carbonate units, a middle, evenly bedded limestone lacking fossil corals, and an upper, irregularly-bedded, stromatoporoid- and/or crinoid debris-rich unit. The Mason City coral faunas are to be found in the lower, biostromal beds and the uppermost, irregularly bedded unit. This upper unit has provided a large number of both colonial and solitary rugosans at the old mill dam on the north edge of Nora Springs (Locality 8, Text-fig. 11), and also wherever exposed along the Shell Rock River southwards, between Nora

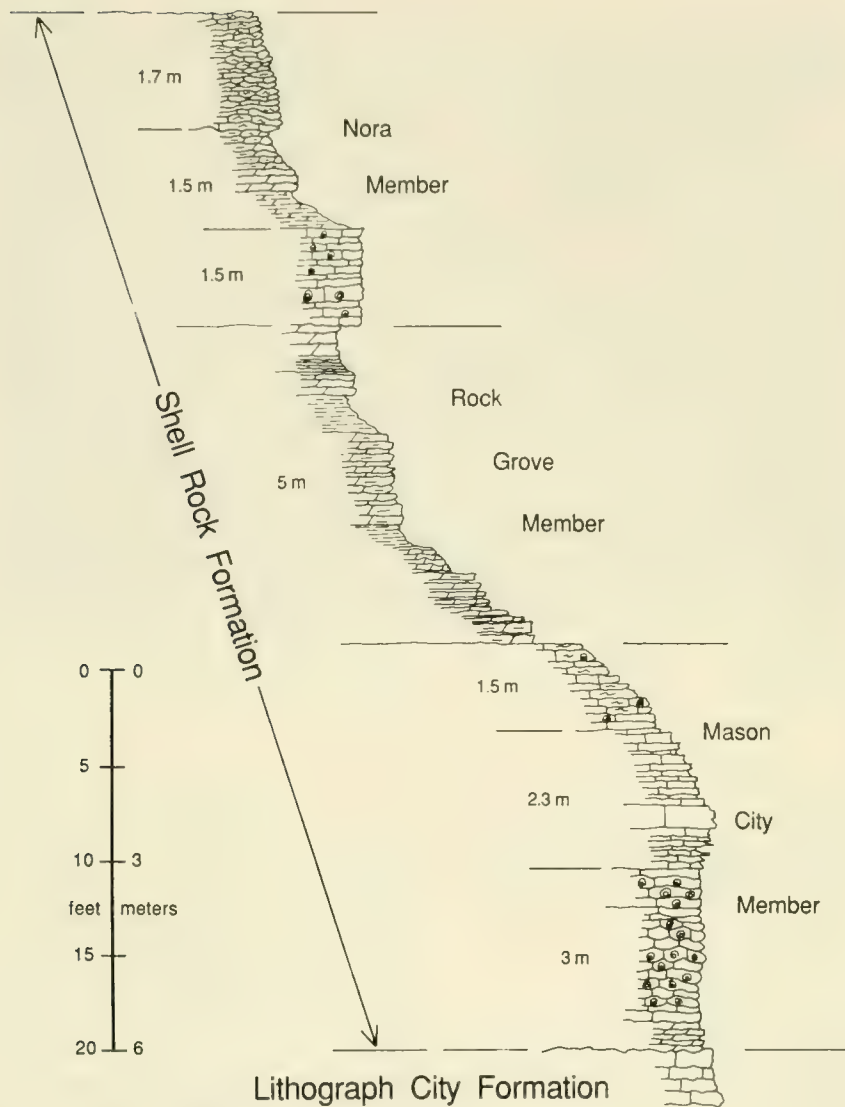


Text-figure 1.—Index map of outcrop area of Frasnian strata in north-central Iowa, as well as symbols for strata exposed at each locality. Further information regarding the locations and strata at each locality is to be found on following text-figures and in the Appendix.

Springs and Rockford. It has yielded abundant solitary corals (*Tabulophyllum*), and colonial phillipsastroid rugosans at Cooper's Bend, at Tom Williams Quarry (Locality 16, Text-figs. 4,6), and as far south as the Maxson Quarry at Marble Rock, Iowa (Locality 24, Text-fig. 9).

ROCK GROVE MEMBER

The Rock Grove Member consists of yellow-weathering dolomitic shale and argillaceous dolomite. The unit commonly forms a somewhat recessive slope with generally poor outcrops. The name Rock Grove Mem-



Text-figure 2.—Composite stratigraphic section of the Shell Rock Formation as it is exposed along the Shell Rock River, from north of Nora Springs to Rockford, Iowa.

Table 1.—Stratigraphic subdivisions of outcropping units of the Shellrock Formation, as slightly modified from Belanski (1927) (Note: Belanski referred to subdivisions of members as zones, referring to what are roughly local range zones of prominent fauna; these are here noted as beds. Some of the taxa utilized above may also be invalid.)

SHELL ROCK FORMATION

NORA MEMBER

"Second *Actinostroma*" beds — upper biostrome

Platyrachella beds — argillaceous, dolomitic

"First *Actinostroma*" beds — lower biostrome

ROCK GROVE MEMBER

MASON CITY MEMBER

Lepidocentris beds

Trigonotreta beds

Aulopora beds — basal biostrome

ber comes from "its great development in Rock Grove township of Floyd County", (Belanski, 1927, p. 328), with a type section along the Shell Rock River, south of Nora Springs, Iowa (for details, see Koch, 1970, p. 12).

The Rock Grove Member does not contain coral faunas, although it is fossiliferous, with upper and lower units recognized by Belanski based on molluscs and brachiopods (1927, p. 328, 330). The only corals reported are from the uppermost bed of the member, as exposed on the east side of the Shell Rock River at Rockford, and reported only as "corals" by Belanski (1927, p. 353). This bed was not observed by me, and only one coral specimen in the Belanski collection at the University of Iowa is labeled as coming from Rock



Text-figure 3.—Outcrops of Mason City Member at its type locality on the east side of the Shell Rock River at Nora Springs, Iowa (Locality 9, Appendix). The indentation near the base of the outcrop marks the base of the Mason City. Photograph taken in 1986 from the bridge where Highway 18 crosses the river on the west side of Nora Springs. The uppermost beds of the member are exposed just to the left of the photograph.

Grove beds at this locality, apparently a new species of *Tabulophyllum* (see below under *T. buccinum* n. sp., a form which was otherwise only found in basal Nora strata.).

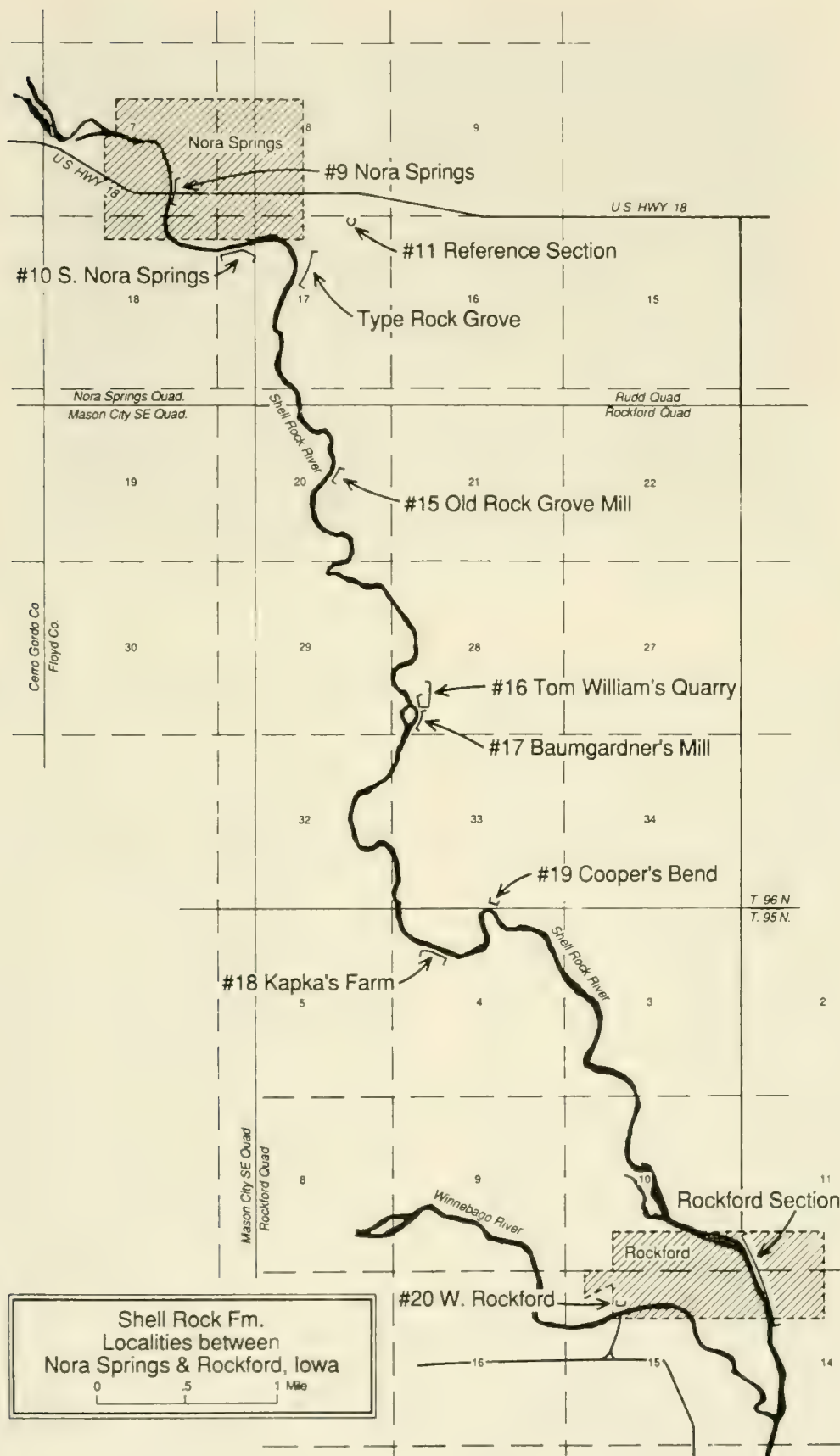
NORA MEMBER

The Nora Member was named by A. O. Thomas (1913, p. 459) for Nora Junction, a former railroad junction on the southwest side of Nora Springs, Iowa (Belanski, 1927, p. 323).

In most outcrops, the Nora Member is very fossiliferous. It was divided, almost on a bed-by-bed basis by Belanski (1927), who named very thin units as zones and zonules on the basis of faunal elements that are only locally prominent. More generally, the Nora Member can be divided into three units, described by Belanski (1927, p. 326) as a lower biostrome, the "First *Actinostroma* zone", a medial shaley unit, and an upper biostromal unit, the "Second *Actinostroma* zone". The Nora Member is thus characterized by extremely fossiliferous lower and upper biostromal units, limestones crowded with stromatoporoids (Text-fig. 10), and commonly also containing rugose and tabulate corals. These beds outcrop best along the Shell Rock River northwest of Nora Springs, where coral- and stromatoporoid-bearing facies occur in what Belanski called the "Reed Creek Phase" (1927, p. 359).

These two Nora biostromes form a series of outcrops along the Shell Rock River, commencing just

north of Nora Springs and extending 5.6 km (3.5 mi) along the river to the north and northwest. The Shell Rock lower member (Mason City) outcrops on the Shell Rock River within the town of Nora Springs as far as the mill dam at the north edge of the town, where the uppermost beds of the Mason City are seen just downstream of the old mill site. Beginning one-fourth of a mile further north, outcrops of the Nora Member are semi-continuous and both biostromes are highly fossiliferous, containing a multitude of rugose corals as well as stromatoporoids, tabulate corals and brachiopods. These are outcrops (Text-figs. 10,11) that were referred to by Belanski (1927, pp. 359–365) as the Reed Creek "Phase", Bjorgason "Phase", Sherman Bluff "Phase" and Keidle Bluff "Phase", progressively from south to north. Belanski used the term "phase" to refer to areas of outcrop which had some internal lithological and/or faunal consistency. In this series of outcrops, the Nora biostromes are persistent (Text-fig. 12). A less characteristic carbonate buildup is seen at Weitsie's Bluff (Text-figs. 12,13) where the lower and upper biostromal units have merged, but they separate again to the north as shown in Section 26 of the township (Locality 1, Text-fig. 12) north of Keidle's Bluff. The variation of the Nora biostromes in outcrops is consistent with their being a varying distance from the carbonate bank recognized by Witzke and Bunker (1984) west of the present outcrop belt in the near subsurface.



Text-figure 4.—The Shell Rock Formation exposures in the region between Nora Springs and Rockford, Iowa. Details of locations and stratigraphic section exposed are to be found in the Appendix.



Text-figure 5. Exposures of the uppermost carbonates of the Mason City Member along the Shell Rock River just downstream of the Nora Dam (Locality 8, Appendix) in the background. These outcrops are the best exposures of the very coralliferous beds of the upper Mason City. Photograph taken in June of 1986.

To the south of Nora Springs, the Nora Member outcrops in an area west of the Shell Rock River (Text-figs. 14,16), as at the former McEachron Quarry at Portland, Iowa (Locality 13), at the county roads quarry (Locality 14), and along the Winnebago River at the west edge of Rockford (Locality 20). Outcrops also include the splendid exposures (Locality 16, Text-fig. 6) at the former Tom Williams Quarry in Section 23, T. 96 N., R. 18 W. (Koch and Strimple, 1973), where a slight downwarp of the strata drops the top of the Mason City Member and brings the outcrop belt of the Nora as far east as Rudd, Iowa (Text-fig. 15). All of these outcrops have yielded abundant fossil rugosans.

LIME CREEK FORMATION

The Lime Creek Formation of north-central Iowa, with its outcrops in Cerro Gordo and Floyd Counties (Text-figs. 16,17), is well known to the many paleontologists who have collected the beautifully preserved and highly abundant faunas of the middle member. These were described by Fenton and Fenton (1924). Specimens of the Lime Creek fauna (or "Hackberry Stage") are to be seen in museums and collections in North America and throughout the world. More recently, outcrops have been considerably degraded by overcollecting, and by covering through slumping and vegetation (Text-figs. 18,19).

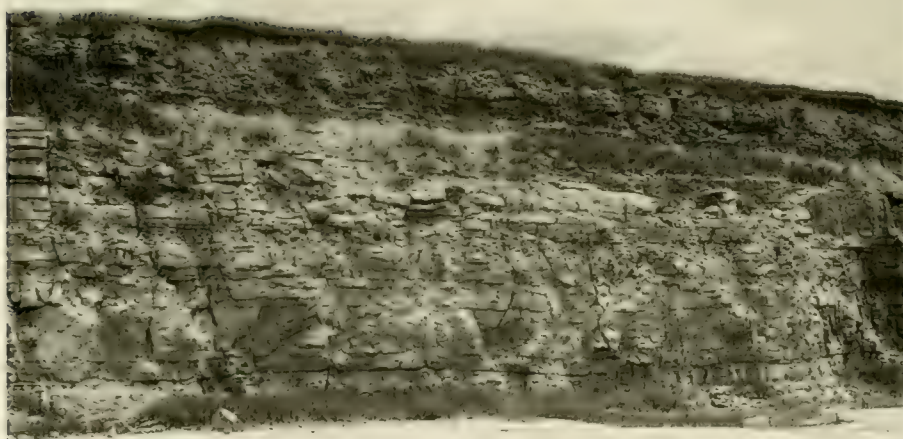
The Lime Creek Formation is subdivided into the basal Juniper Hill Member, medial Cerro Gordo Member, and upper Owen Member (Text-fig. 19). As the

Juniper Hill Member does not contain any corals on the outcrop, it will not be discussed in this paper, except to note that it formerly was used in the manufacture of brick and tile, both at Mason City and at Rockford, Iowa. It is a pure clay shale, and bluish where fresh. The thickness shown for the Juniper Hill in Text-figure 20 is only the amount exposed at the Rockford Brick and Tile Co. claypit at Rockford, Iowa in 1967 (Text-figs. 21,22). The unit is undoubtedly much thicker, with a maximum of 21 meters estimated by Day (1990, p. 615).

The name Lime Creek was proposed by Calvin (1896) for the unit as exposed along the banks of the Winnebago River (formerly named Lime Creek), at what is now Claybanks Conservation Park (Locality 28, Text-Fig. 16). Although the name of Lime Creek was subsequently altered, the type section lies only 1.2 km ($\frac{3}{4}$ mi) south of Little Lime Creek (Mason City S.E. Quadrangle), and use of this name should entail no difficulty. This locality also served as the type of the "Hackberry Stage" of Fenton (1919, p.355), as it is within the area then called Hackberry Grove. The type section, as exposed in 1968, is illustrated in Text-figure 23.

CERRO GORDO MEMBER

The shaley, highly fossiliferous beds of the Cerro Gordo Member of the Lime Creek Formation are exposed in a series of natural and artificial cuts through the low hills forming a belt 5–6 km (3–3.5 mi) wide



Text-figure 6.—Shell Rock Formation on east wall of Tom Williams Quarry, Locality 16 (Appendix), with almost complete section of Mason City Member forming cliff overlain by slope forming Rock Grove Formation above, which is in turn overlain by the lower biostrome of the Nora Member at the top. Photograph taken in 1967.

extending south and southwest of the Winnebago River, from Owen Grove on the west (Text-fig. 16) to Rockford on the east (Text-fig. 17). To the west and northwest of Owen Grove, the dominant facies of the sequence is dolomitic, so that when the unit was seen at Mason City, all fossils were preserved as molds, and are not of interest for study of coral faunas.

The stratigraphic sequence reported by Fenton and

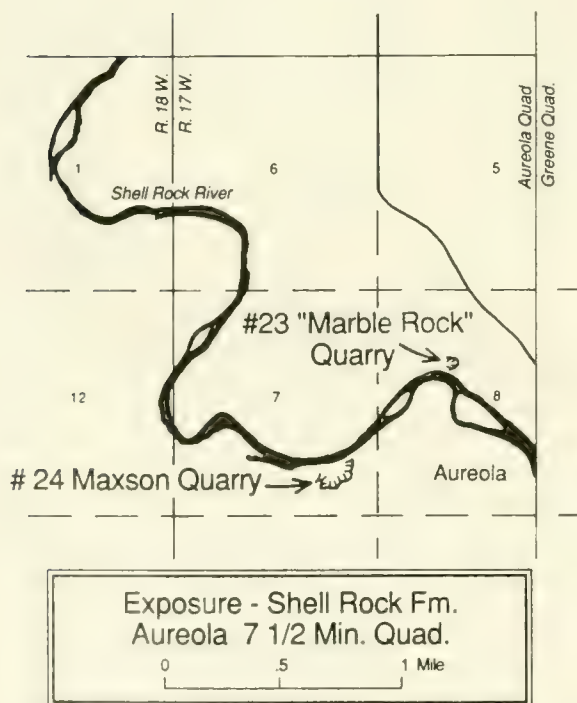
Fenton (1924, p. 8) is superficially biostratigraphic, although not in a modern sense, as presented below under the heading of biostratigraphy. Fenton and Fenton divided the Cerro Gordo Member (or substage as they called it) into an upper “*Spirifer* zone” and a lower “*striatula* zone”. These are traceable lithic units. Each of their “zones” was divided into a series of “faunules”, some restricted to a single layer, (e.g., the *Lep-*



Text-figure 7.—North to south cross section of the Mason City Member of the Shell Rock Formation between Nora Springs on the north and Greene (Marble Rock Quarry) and Roseville, Iowa on the south and southeast. Changes in thickness in the Mason City Member appear most closely related to variation on the basal disconformity surface. Localities shown on this section are illustrated on maps of Text-figures 3 and 4.



Text-figure 8.—Exposures of the entire Mason City Member at Cooper's Bend (Locality 19, Appendix). The massive dolomites forming the shelf at the base of the sequence are underlying Cedar Valley beds, with 1.3 m (4 ft) of Mason City divided into lower shaley, rubbly coral-bearing limestones and upper more massive unit, in turn overlain by slope-forming shaley beds of the Rock Grove Member under trees. Photograph taken in June, 1986.



Text-figure 9.—Exposures of the Shell Rock Formation along the Shell Rock River northwest of Greene, Iowa. Further details of stratigraphic localities are noted in the Appendix.

tostrophia "faunule", 7.5 cm thick, which is one thin bed characterized by the small, concavo-convex brachiopod *Nervostrophia*). Such units are only locally recognizable, and are not of use as zones. Text-figure 23 shows lithologic correlations of Cerro Gordo units within sections described between Owen Grove and Rockford.

Several marker beds aid in the correlation and recognition of portions of the member, often allowing precise placement of a very limited outcrop sequence within the stratigraphic framework of the entire unit. Remarkable uniformity exists within this member in its area of outcrop, facilitating correlation. One such bed is the "rusty" bed, shown at the base of the upper unit ("*Spirifer*" zone of Fenton, 1919), at the type section in the bluffs along the Winnebago River (Locality 28, Text-figs. 16,17). This bed is hematitic, due to the oxidation of pyrite on what apparently was a hard ground. It is characterized at the type section by a great abundance of stromatoporoids and stromatoporeid-coated colonies of *Pachyphyllum*, *Hexagonaria*, *Iowaphyllum*, and the tabulate genus *Alveolites*. The bed can be recognized as far west as roadcuts along County Highway D, south of Portland, Iowa (Locality 27, Text-fig. 16), and maintains its essentially rusty, stromatoporeid and coralline nature eastward as far as the Cerro Gordo-Floyd County line. Although the nature of the unit is altered somewhat, it occurs as



Text-figure 10.—Closeup of large stromatoporoid in lower Nora biostrome at level of hammer, with dolomites of the Rock Grove (?) Member underlying. Outcrop is along west side of Shell Rock River at Reed Creek, Locality 4 (Appendix). Photograph taken in 1986.

a prominent limestone unit (0.7 m) at the base of the upper unit of the Cerro Gordo at the former claypit of the Rockford Brick and Tile Co. (Text-fig. 23). The strata overlying this unit and below the basal beds of the Owen Member are the source of virtually all corals from the Cerro Gordo Member. No corals, solitary or colonial, were collected from outcrops of the underlying unit (“*striatula* zone” of Fenton and Webster, in Fenton and Fenton, 1924, p. 8), which is characterized by an abundant brachiopod fauna and overlies the Juniper Hill Member, with clay nearly barren of megafossils.

Fenton and Fenton emphasized that light tan-weathering shales containing a large number of *Strophonellodes* and *Douvillina* (their *Leptostrophia canace* bed) is very useful for correlation of Cerro Gordo strata. It occurs approximately three meters below the top of the member. I was not able to trace this bed with confidence. The “furoid beds” of Fenton and Fenton (1924, p.13) are also not reliable as marker horizons,

as many of the sandy or shaley limestone units of the upper middle part of the member develop a similar burrowed aspect, with the trace fossil *Gracilirectus* Webster present at many localities. For example, 1.2 km (¾ mi) southeast of the main Bird Hill locality, an outcrop exposes equivalent beds in which three separate limestone units show extensive burrowing (Locality 32, Text-fig. 17). At a hillside outcrop and road cut 0.8 km (0.5 mi) south of Locality 27 is one limestone bed (2 m above the “rusty bed”), also extensively burrowed, that could easily be mistaken for the “*Gracilirectus* bed”.

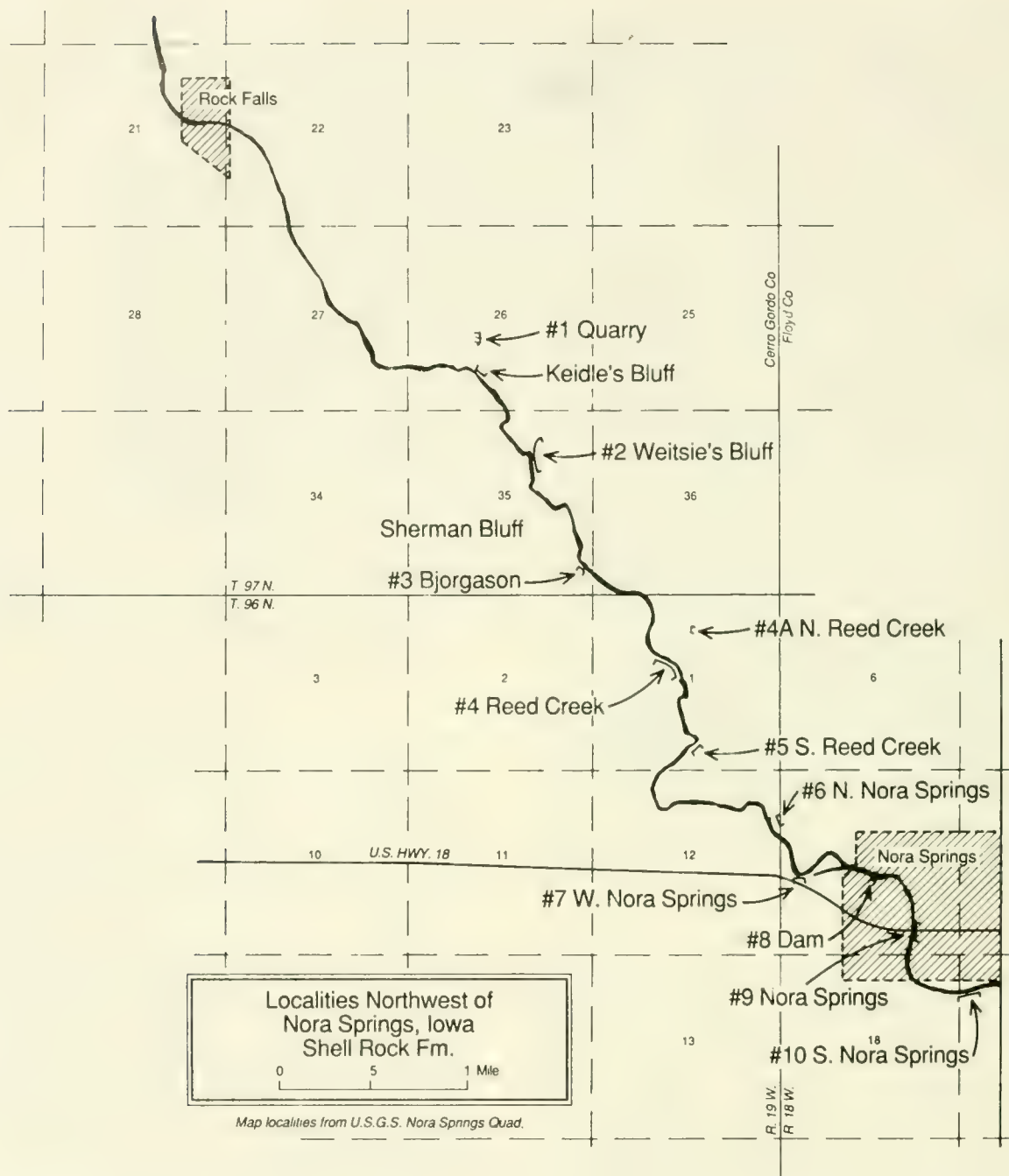
In summary, the Cerro Gordo Member is a sequence of calcareous shales and argillaceous nodular limestones, with a lower unit (approximately 4.5 m at Rockford) characterized by calcareous shales bearing abundant brachiopod faunas, and an upper unit (approximately 10 m thick) characterized by an alternation of calcareous shales and nodular argillaceous limestones bearing the prolific coral and brachiopod faunas of the member. This unit is overlain by the carbonate rocks of the Owen Member. Lithologies of the Cerro Gordo Member are quite constant over its limited area of outcrop (Text-fig. 23).

OWEN MEMBER

The type section of the Owen Member of the Lime Creek Formation appears to be somewhat unusual for this member, which can be traced south from Cerro Gordo County into Butler and Franklin Counties (Text-fig. 24). The type sequence of limestones of the basal *Idiostroma* beds, along with overlying soft dolomites and dolomitic shales of the *Floydia* beds, is partially exposed in the western part of Section 31 of Portland Township (Locality 26 and in the eastern part of section 26 of Mason Township (Locality 25) along a small creek tributary to the Winnebago River (Text-fig. 16). The northern facies of the *Mourlonia* beds seen at Owen Grove also changes rapidly to the south and southwest and is developed as a biostromal facies with highly abundant *Actinostroma* at Rockwell and at the Lillibridge Quarry, southeast of Rockwell (locs. 36 and 38), as shown on Text-figure 24, (and localities shown in Text-fig. 25). Farther south, exposures were formerly excellent in the Buseman and Carolus quarries south of Dumont, Iowa (Text-figs. 26–28).

BASAL BEDS (“*Idiostroma* zone” of Fenton, 1919, p. 364)

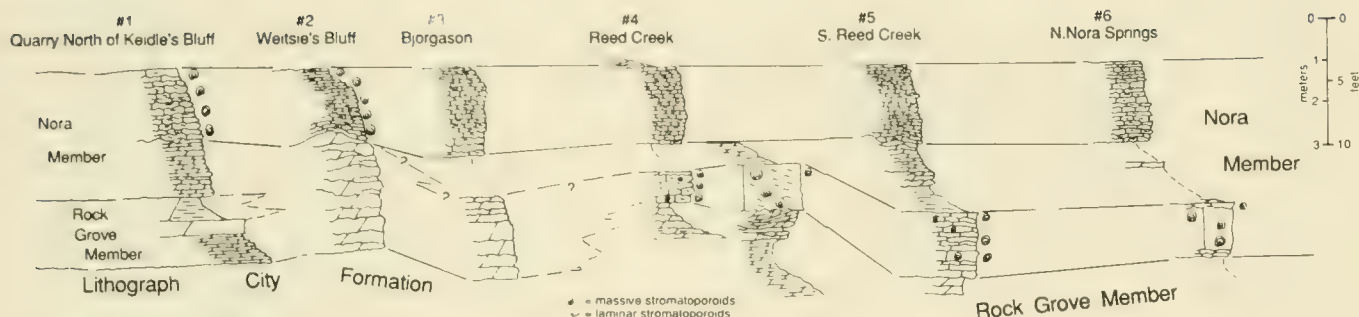
Well-bedded micritic limestones containing abundant branching stromatoporoids (*Amphipora*, according to Stock, 1984, p. 128) are present in the type section at Owen Grove, and are characteristically developed through all of eastern Cerro Gordo County,



Text-figure 11.—Localities where the Shell Rock Formation was studied along the Shell Rock River northwest of Nora Springs, Iowa. Sections 1–7 are of the Nora Member, while the lower part of the formation is also exposed in the area around and to the south of Nora Springs. Further details are to be found in the Appendix.

capping hills developed on the calcareous shales and argillaceous limestones of the Cerro Gordo Member. The *Amphipora* beds are seen at Bird Hill, Hackberry Grove, and in all intervening areas. The same facies also occurs at the Morgan Quarry in northeastern Franklin County (Text-fig. 29), with thinner, but identical *Amphipora*-bearing limestones forming the base

of the Owen Member. Farther south, in Butler County, argillaceous micrites apparently contain *Amphipora*, but these beds differ from the more typical basal Owen in that they weather to a recess below more massive overlying beds and contain branching bryozoans and *Amphipora* (see Buseman and Carrolus sections, Text-figs. 24, 26–28).



Text-figure 12.—Stratigraphic section illustrating changes in the Nora Member in a northwest to southeast traverse along the Shell Rock River north of Nora Springs, Iowa. Localities are those first studied by Belanski, and further information on localities is shown on Text-figure 6, and listed in the Appendix.

MIDDLE BEDS ("Floydia zone" of Fenton and Fenton, 1924, p.8)

The *Floydia* beds, named for their fauna of large gastropods, are variable in the area studied. At the Owen Grove type section, these soft brown dolomites are poorly exposed. To the southwest at Rockwell, in the abandoned quarry which serves as the town dump (Locality 36, Text-figs. 24,25), the lower 2 m of the unit is composed of a biostrome with highly abundant stromatoporoids comprising up to 99% of the rock. Above are found bedded argillaceous dolomites with a very abundant fauna of *Hexagonaria bassleri* in the uppermost 0.5 m. This upper unit changes very shortly to the south, and in Linn Grove Park, in the town of Rockwell, two abandoned quarries show up to 3.2 m of biostromal beds (Locality 37, Text-fig. 25). This facies change takes place in approximately 1.2 km (0.75

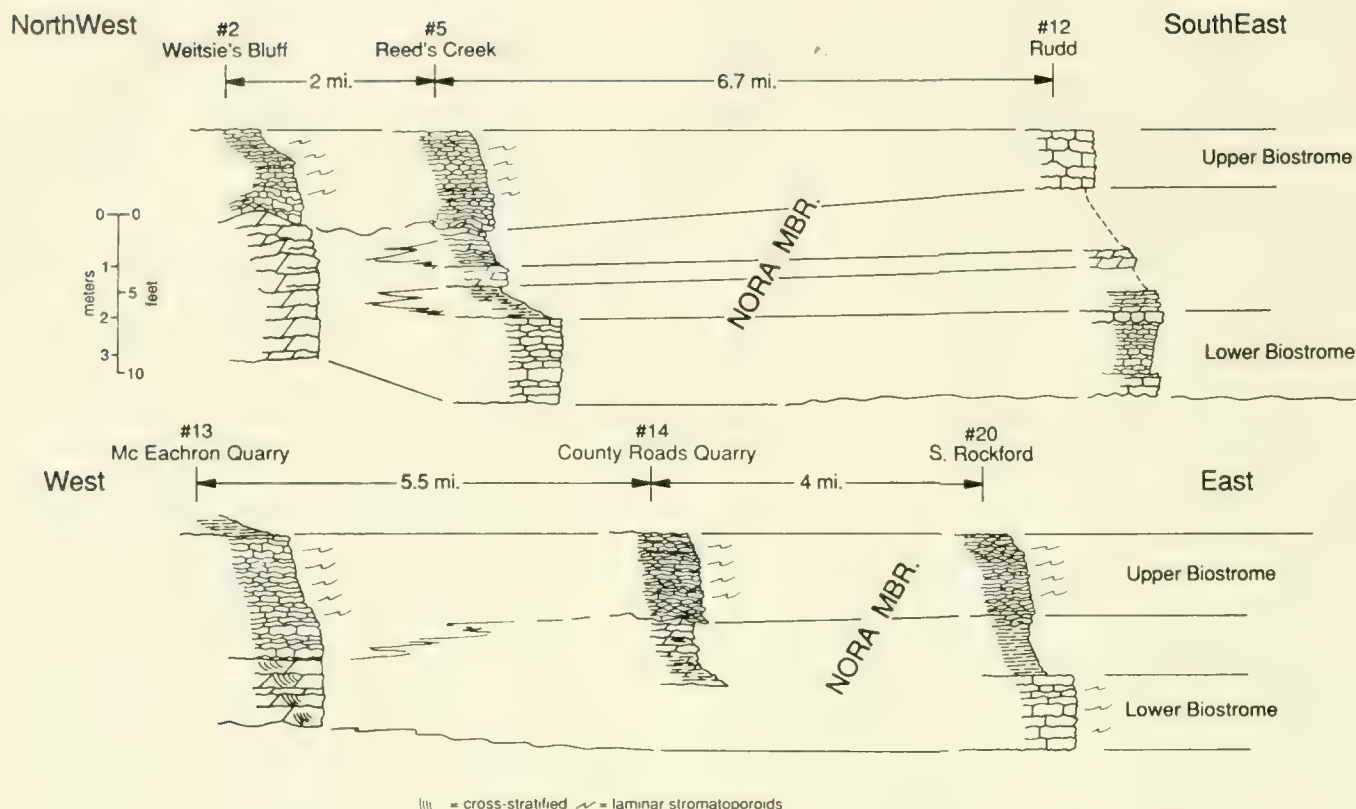
mi). The biostromal facies of the *Floydia* beds are best shown at the Lillibridge Quarry, south-southeast of Rockwell, where stromatoporoids account for virtually all of the volume of the main biostrome (4 m thick, Text-fig. 24).

To the southeast, at Morgan Quarry in Franklin County (Text-figs. 24,29), *Floydia* beds are rather different in aspect. The lower 2.1 m of the unit are composed of calcareous shales and cross-stratified biomicrite bearing a fauna of *Pachyphyllum*, *Tabulophyllum*, *Cyrtospirifer*, and crinoid columnals. This unit is represented by burrowed micrites farther southeast at the quarries located south of Dumont in Butler County.

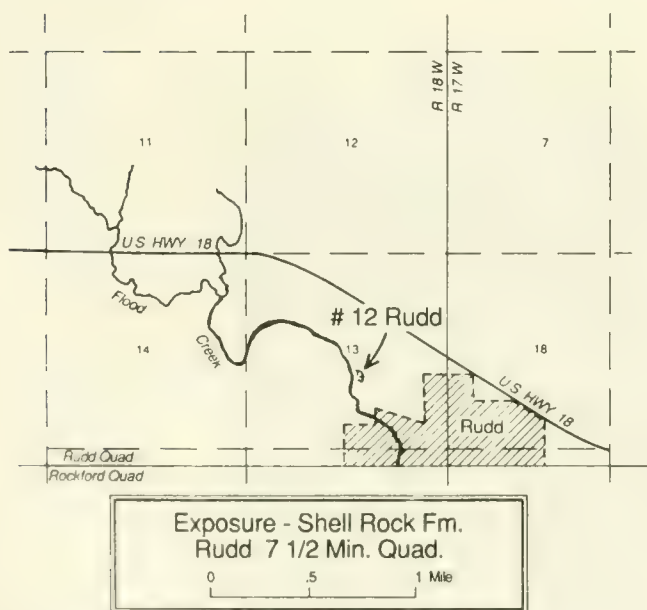
Southeast of the thick biostromal development in the Rockwell area, fossiliferous micrites and coarser bioclastic limestones comprise the upper part of the *Floydia* beds. This unit contains abundant subspherical



Text-figure 13.—Nora Member at Weitsie's Bluffs, Locality 2 (Appendix), with thick massive carbonate facies of complete(?) Nora sequence, which here lies directly on pre-Shell Rock beds. Photograph taken in 1986.



Text-figure 14.—Two stratigraphic sections of the Nora Member are shown; the upper section illustrates stratigraphic changes as one traverses away (east) from the more massive calcareous facies of the Nora, as would be seen in the subsurface shortly to the west of the outcrop belt. The lower section illustrates similar facies changes from Portland to Rockford, with a similar more distinct development of the two biostromes of the Nora Member in the eastern area (Localities are shown on Text-figures 3,11).

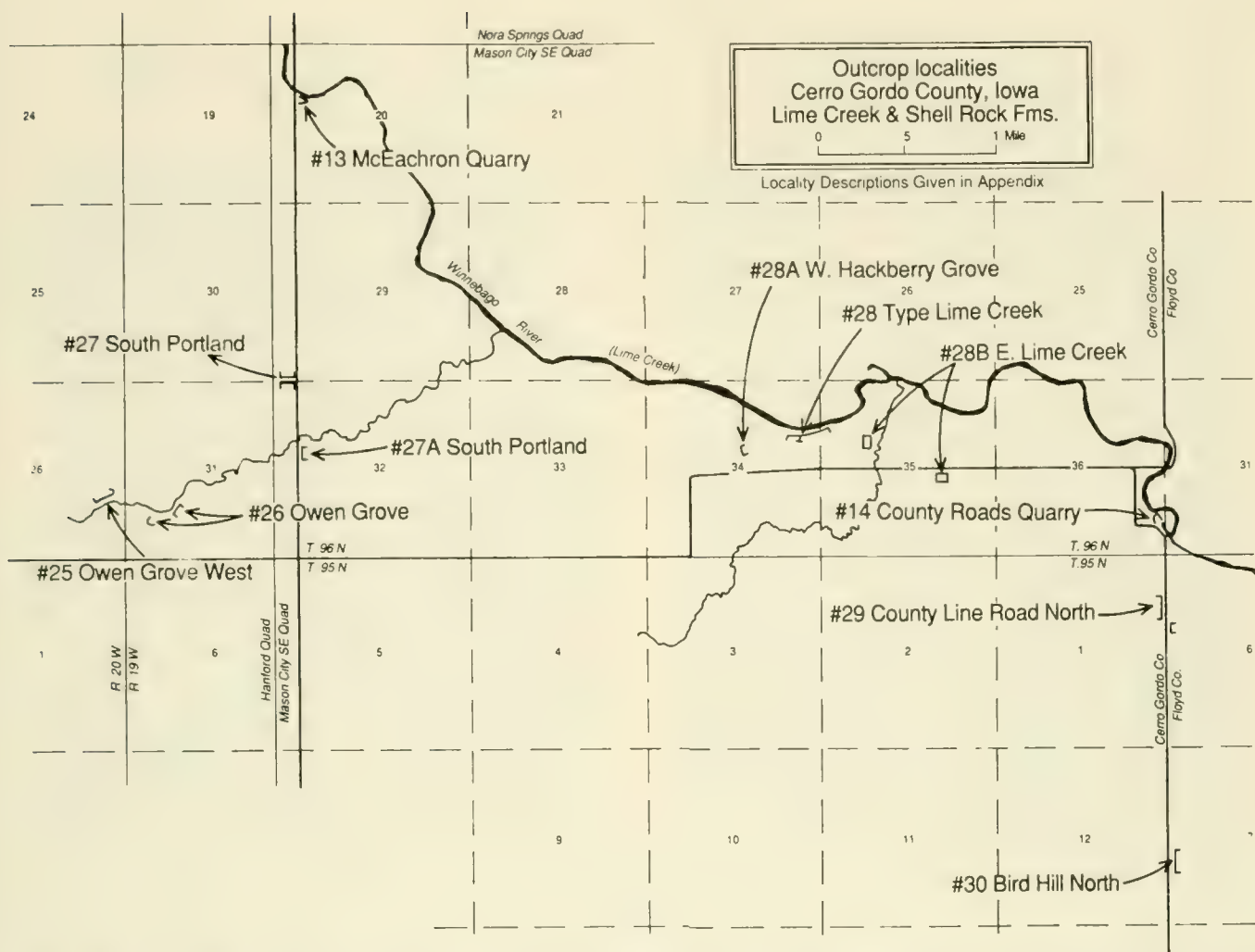


Text-figure 15.—Location of exposure of Nora Member at Rudd, Iowa. Further details are in the Appendix.

stromatoporoids and at several levels is biostromal in aspect (Text-fig. 24). This is the source of much of the coral fauna of the lower part of the Owen Member. The upper portion of this middle unit is generally speaking, dolomitic and argillaceous. The unit is soft, and weathers into slopes between the carbonate units below and above. It is characterized by gastropod and pelecypod faunas and characteristic spiriferid and chonetid brachiopods. Its soft, dolomitic nature makes it an easily recognizable unit where it is exposed.

UPPER BEDS ("Acervularia zone" of Fenton, 1919, p. 366)

This thin unit of light gray-weathering micrites is easily recognized and bears the most abundant coral faunas of the Owen Member. An average thickness approximates that seen in western Owen Grove, where well-exposed beds are 0.9 m. The unit is never thick, but has been the source of most of the coral species described from the Owen Member. The single exposure that contributed most specimens is the now-aban-



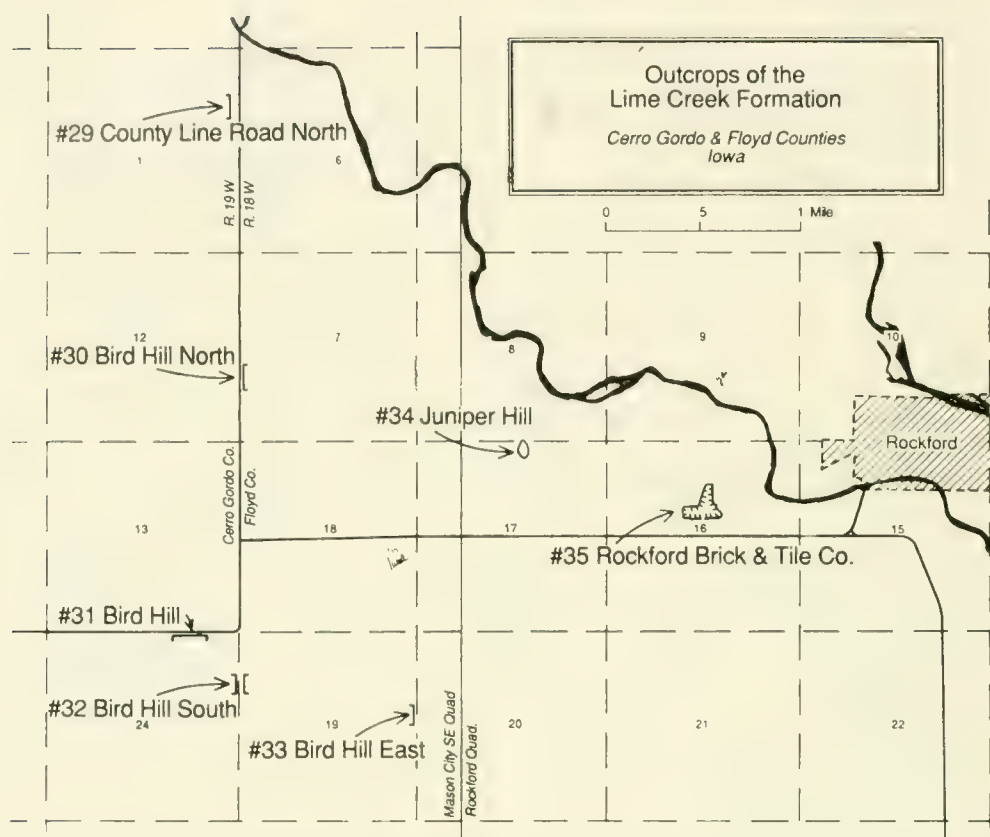
Text-figure 16.—Outcrop localities of the Lime Creek and Shell Rock Formations along the Winnebago River and its tributaries. Section number 28 is the type section for the Cerro Gordo Member of the Lime Creek and number 26 is the type locality for the Owen Member. Further information is in the Appendix.

doned quarry in Owen Grove (Locality 26, Text-fig. 16). Stripped surfaces at the Lillibridge Quarry south-east of Rockwell (Locality 38, Text-fig. 25) provided very abundant specimens of *Hexagonaria bassleri* and *Pachyphyllum crassicoatum* as well as numerous tabulate and solitary corals.

BIOSTRATIGRAPHY

The Lime Creek corals have long been regarded as one of the major Frasnian coral faunas of the world, but it is only during the past decade that an easily correlated zonation of the Shell Rock and Lime Creek beds has been worked out, primarily on the basis of conodonts and brachiopods. The coral faunas of the Shell Rock and Lime Creek Formations are not nearly as useful as conodonts or brachiopods for zonation of these strata, but are listed in Table 2 with their strati-

graphic position in the major subdivisions of the sequence. Unit 1 shown on Table 2 is the Mason City Member of the Shell Rock, which Day placed in his *Tenticospirifer shellrockensis* Zone and the lowermost part of his *Strophodonta cicatricosa* Zone (1989, 1996). Corals generally derive from lower, biostromal beds with abundant stromatoporoids, but abundant corals are also found within soft limestones in the uppermost part of the Mason City Member. Unit 2 contains the lower and upper biostromes of the Nora Member, placed in the *Strophodonta cicatricosa* Zone (Day, 1989, 1996). Both biostromes contain abundant corals and stromatoporoids. Within the Lime Creek Formation, Unit 3 of Table 2 is the Cerro Gordo Member, but in actuality all of the Cerro Gordo corals come from the upper part of the member which Fenton and Fenton called the "*Spirifer zone*" (1924), the *Cyrtos-*



Text-figure 17.—Outcrops of the Lime Creek Formation, largely only of the Cerro Gordo Member, except for Bird Hill, where the basal portion of the Owen Member also outcropped. The Rockford Brick and Tile Company is no longer (1997) actively quarrying the Cerro Gordo and underlying Juniper Hill Members. Further locality information is contained in the Appendix.

pirifer whitneyi Zone of Day (1996). Unit 4 is the Owen Member, in most part the uppermost Owen, formerly referred to as the “*Acervularia* zone” (Fenton and Fenton, 1924), now placed in the *Iowatrypa owenensis* Zone of Day (1996) on the basis of its brachiopod fauna. Corals are scattered throughout the Owen, especially where stromatoporoid biostromes are present, but are most abundant in the top meter of the unit.

In 1989, while placing the Shell Rock Formation in the Cedar Valley Group, Witzke *et al.* also formally proposed the Lithograph City Formation for Cedar Valley beds that everywhere underlie the Shell Rock in north central Iowa (1989, p. 241). The understanding of the biostratigraphy of these Frasnian formations of Iowa has been greatly advanced by the work of Day on both conodont and brachiopod faunas of these strata from north-central Iowa. His summary of applicable brachiopod and conodont faunas of these beds also indicates how they are correlated with the Frasnian Composite Standard, as developed for the Montagne Noire sequence by Klapper (1989). As a result of Day’s work, as well as that of earlier studies, the units

of the Shell Rock and Lime Creek formations have now been carefully classified by their faunas.

Day summarized the ages of units in this sequence on his figure 3 (1996, p.281). The Shell Rock Formation is placed in lower half of the Frasnian Stage, with all but the uppermost beds of the Mason City Member belonging in the *Tenticospirifer shellrockensis* Zone, while the uppermost Mason City, the Rock Grove and Nora members belong in the *Strophodonta cicatricosa* Zone. The Shell Rock Formation contains an undiagnostic conodont fauna, but physically overlies the upper member of the Lithograph City Formation, which is correlated to the Montagne Noire (M.N.) Zone 4 of Klapper (1989). At present, the conodont faunas of this interval cannot be correlated with the Frasnian zones established in offshore sequences as represented in the Montagne Noire. The Nora Member still contains this undiagnostic conodont fauna, but underlies the Juniper Hill Member of the Lime Creek Formation, placed in the *Lingula fragila* Zone (Day, 1996, p. 280), which correlates in largest part to M.N. Zones 9 and 10, and in part to lower Zone 11 of Klapper (1989). On this figure, the Lime Creek Formation



Text-figures 18 and 19.—Photographs to illustrate difference in quality of the outcrop of the upper part of the Cerro Gordo Member of the Lime Creek Formation at Bird Hill (Locality 31, Appendix). Figure 18 was taken in August of 1967 when stratigraphic sequence was clearly exposed, with the basal *Amphipora* limestones of the Owen Member present at the extreme top of the outcrop. Figure 19 was taken in June of 1986 and illustrates the amount of slumping present, and resultant deterioration of the outcrop, where no fossils could be collected in place.

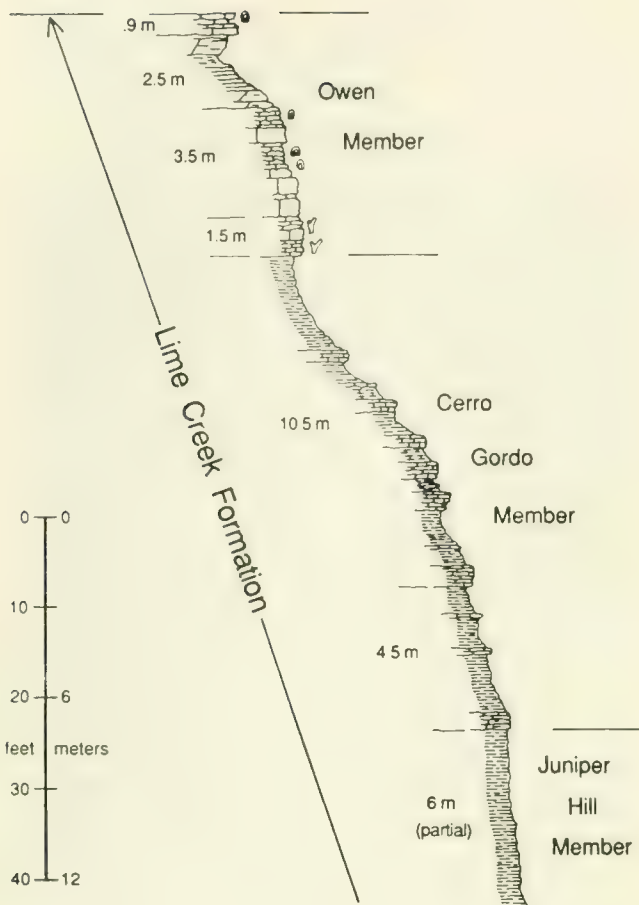
is shown extending from M. N. Zone 9 at the base (Lower Juniper Hill Member) to M.N. Zone 12 at the top of the Owen Member. The Owen Member (with its brachiopods placed in the *Elita inconsueta* and *Lowatrypa owenensis* zones) comprises almost all of M.N. Zone 12 of Klapper (1989), along with the uppermost part of the Cerro Gordo Member (the *Elita inconsueta* Zone). The *Cyrtospirifer whitneyi* Zone, together with the underlying *Douvillina arcuata* Zone and *Nervostrophia thomasi* Zone are correlated to M.N. Zone 11 (with the exception of the basal portion of the latter). For details of this biostratigraphic zonation of the Frasnian of Iowa, the reader is referred to the excellent summary by Day (1996, pp. 277–290). The base of the Famennian Stage occurs somewhat higher in the Devonian sequence in northern Iowa, at the base of the overlying Sheffield Formation (Witzke and Bunker, 1996, p. 319).

FIELD CONDITIONS

The greatest part of field work for this study was done in the summers of 1967 and 1968; both strati-

graphical, including description of stratigraphic sections, and paleontological, collecting faunas. Additional collecting was done in 1970. Most collections during this time were made in place in the stratigraphic subdivisions shown in stratigraphic sections, with large collections of fossils from float only made in the Rockford Brick and Tile Company's piles of stripped Cerro Gordo beds at their quarry.

Ten days spent in the field in June of 1986 demonstrated the impossibility of carrying out the same type of detailed stratigraphic field research at present, as few quarries and roadside exposures remain in their previous state (Text-figs. 17,18). There appear to be several factors influencing the quality of outcrops of these units, including rainfall and resultant vegetation, and road-building activities and their effect on limestone quarrying for road metal. Also, the demise of the Rockford Brick and Tile Company, and its excavation of Juniper Hill Shale has had a major effect on the availability of Lime Creek fossils. Stripping and quarrying resulted in constant creation of new outcrop



Text-figure 20.—Composite stratigraphic section of the Lime Creek Formation. The thickness of the Juniper Hill Member is only that which was exposed at the Rockford Brick and Tile Company in 1968. The Cerro Gordo and Owen Members are illustrated as they were at their type sections at Hackberry Grove and Owens Grove. Further details on localities are seen in text-figure 11 and in the Appendix.

and new stripped surfaces in the Cerro Gordo Member as long as the quarry was in operation (Text-figs. 20,21).

SYSTEMATIC PALEONTOLOGY

INTRODUCTION

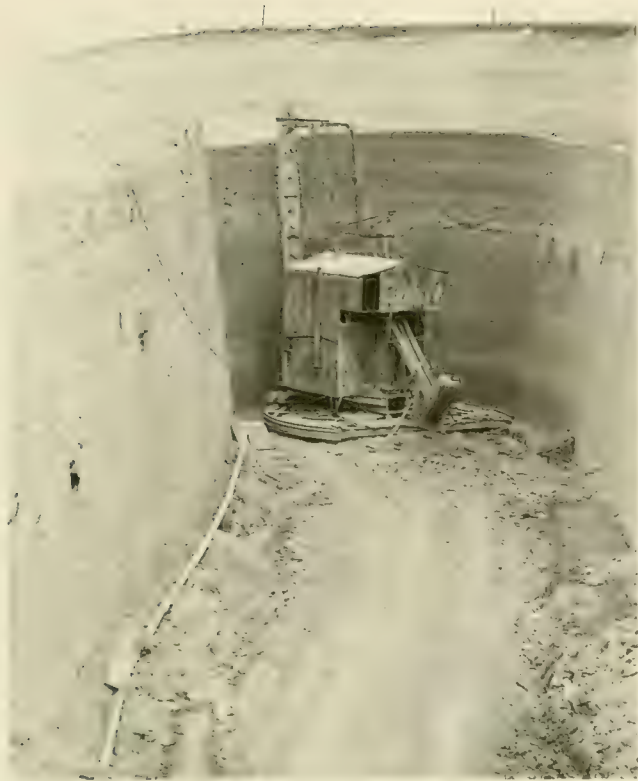
The starting point for my systematic work in Paleozoic corals is the 1981 Revision of the *Treatise on Invertebrate Paleontology* by Dorothy Hill, dealing with the Orders Rugosa and Tabulata. The present study of Iowa corals uses the family-level and much of the genus-level classification of Hill (1981). Hill's generic diagnoses have also been used except as specifically modified (and so noted), or where specifically disagreed with, and so stated in the text. In addition to the *Treatise* nomenclature, I have used morphological terms as defined for rugosans according to the

meanings stated in the Glossary of Terms included in the *Treatise* volume on the Rugosa (Part F, Revised, 1981, p. F32). Where I have utilized terms not included in the Hill glossary, I have referred to other published work or have clarified usage in appropriate places.

One is forced to make a number of basic paleontological decisions when studying species and populations of Paleozoic rugose corals. Variation is potentially immense within populations, species, and biogeographic or ecologic groupings, but commonly is not clearly demonstrable. In addition to difficulties generated by genotypic and ecotypic plasticity, one also must work within a taxonomic framework generated over a number of years by earlier workers, some of whom labored under serious technological, linguistic, or conceptual handicaps.

Species of Late Devonian Rugosa are treated as comprising morphologically cohesive intergrading populations of corals that were restricted in their time span and morphological limits by an unknown but variable amount. I follow the opinion that although these fossil species can only be recognized morphologically, students of the Rugosa should expect variation within populations of fossil coral species approximating that seen within modern and fossil species of the Scleractinia, the septate corals of Mesozoic and Cenozoic time. This is an extremely difficult point to state precisely, but it does indicate that species cannot be satisfactorily understood by study of a small number of specimens, nor can descriptions of taxa based *entirely* on one or a few type specimens adequately define populations or species of these variable organisms. In this study, a number of species have been synonymized that were originally described without the benefit of adequate thin sections or assemblages. Since paleontological publications are only progress reports on our understanding of fossil species, I expect future revision of taxa defined on the following pages.

My natural inclination is to treat fossil species from the point of view of the taxonomic "lumper". Thus, where three species, such as *Iowaphyllum johanni*, *I. marginatum*, and *I. multiradiatum* have been described from a single, 0.5 meter-thick bed in the Cerro Gordo Member from three outcrops with a maximum geographic separation of approximately 9.6 km (6 mi), it seems most logical to approach the population to try to learn whether too many taxa have been named. This differs somewhat from approaching fossil populations seeking peculiarities that might indicate new or undescribed species. Given an elementary understanding of variation in living corals, one cannot systematically study the taxonomy of Frasnian coral species without synonymizing some pre-existing species. These were



Text-figures 21 and 22.—Photographs taken in 1968 illustrating the method of digging clay at the Rockford Brick and Tile Company Quarry (Locality 35, Appendix). Figure 21 shows equipment used to dig clay and load it into trucks at claypit. The freshly dug face exposed 6 meters of the Juniper Hill Member below, and the basal 4.5 meters of the Cerro Gordo Member above. Figure 22 shows a slightly weathered face of the lower Cerro Gordo with its basal silty unit (marked by the presence of the brachiopod *Gypidula*) above the Juniper Hill. Above the lower Cerro Gordo (*Douvillina* zone, with the *Lioclema* bed at the top), the upper part of the Cerro Gordo (so-called *Spirifer* zone) was stripped back to allow ease of quarrying. This is the most fossiliferous portion of the Cerro Gordo, and fossils could be collected in place in the background where each bed was exposed in sequence, or fossils could be collected from this unit in piles of stripped material.

commonly established on the basis of type specimens only, and sometimes on external characters, or on growth characteristics known to vary greatly in living coral populations.

At another level, genera are regarded as convenient names for groups of similar, apparently related, species. There is a tendency among some coral taxonomists to utilize genera in the sense of “superspecies”, where genera are expected to be easily identifiable on the basis of a few morphological characters. Where species are variable and boundaries between species are difficult to define, it is to be expected that genera consisting of these variable species will likewise be difficult to define on the basis of one or a few characters.

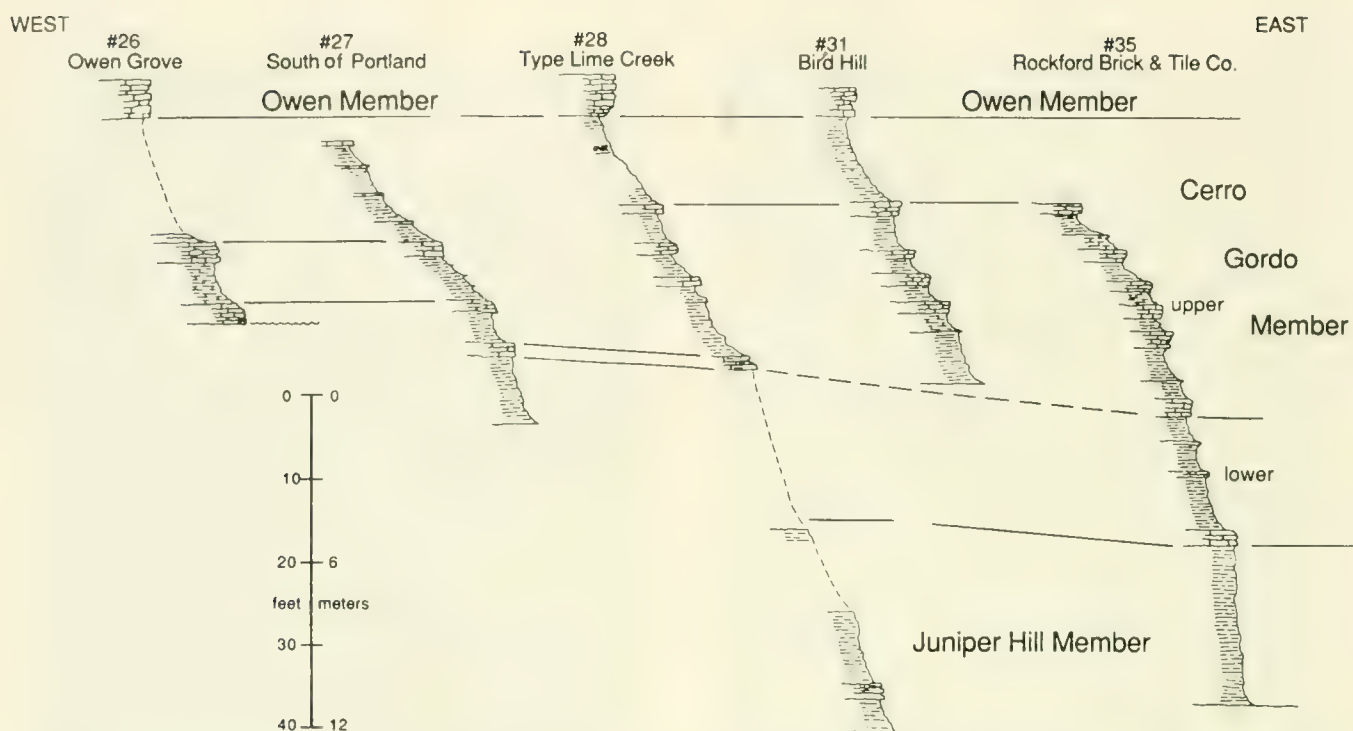
In the systematic paleontology that follows, species are identified on the basis of populations where possible. Where samples were small, but no affinity for it can be determined, the species is listed as “species A”, signifying that no known species can be found, but

additionally that a sufficiently large sample needed to define a new species is not available.

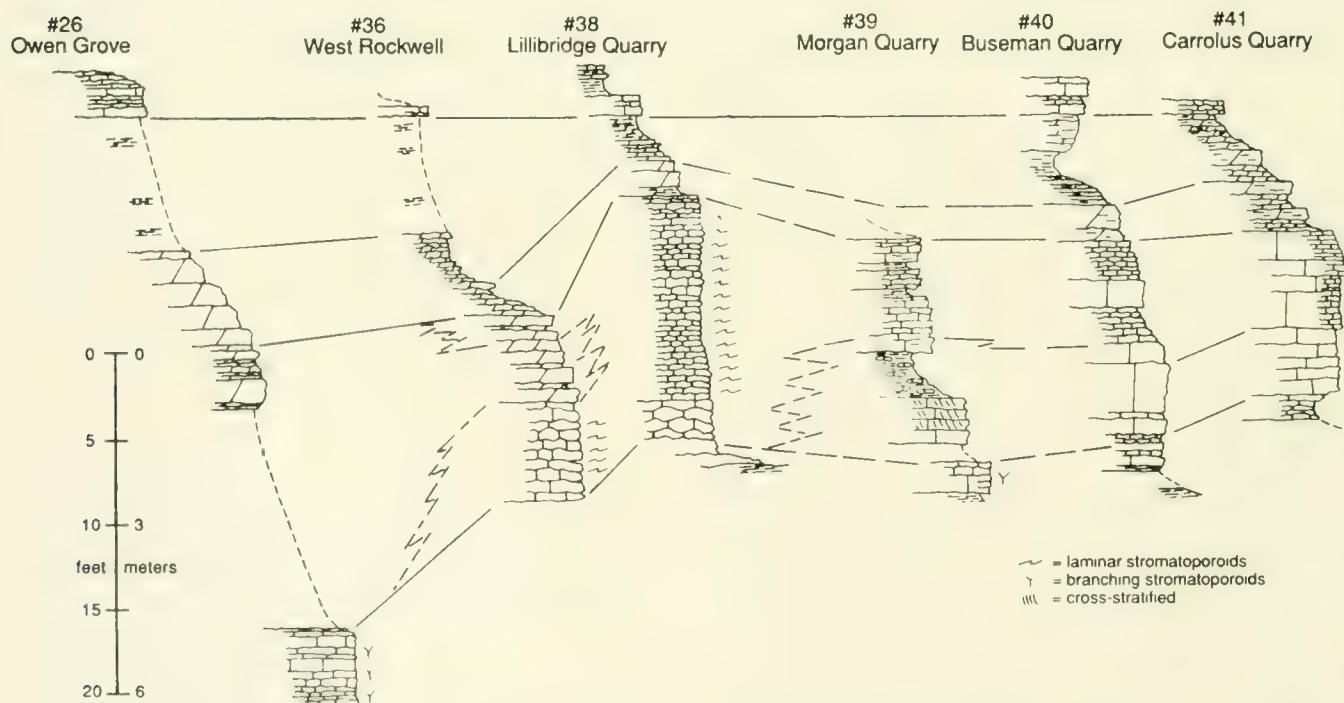
The suprafamilial nomenclature is taken directly from the Hill (1981) revision of the Rugosa of the *Treatise on Invertebrate Paleontology*. Names of authors of these taxa are as listed in the Treatise, and references to their original publication have not been included in the list of references cited that follows this text.

REPOSITORIES

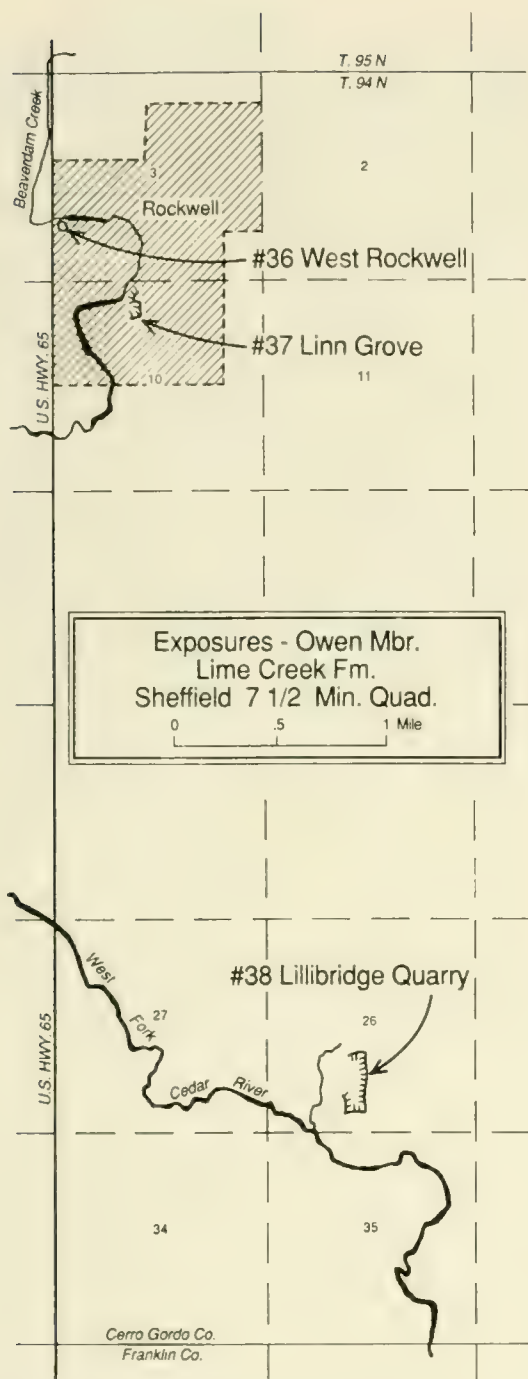
Hall and Whitfield types are in the New York State Museum in Albany, N.Y. (NYSM). The Fenton and Fenton collections are either at the University of Michigan Museum of Paleontology at Ann Arbor, Michigan (UMMP), or at the Field Museum of Natural History in Chicago, Illinois (FMNH). The latter were formerly at the Walker Museum of the University of Chicago, and are on permanent loan to the Field Museum. Belanski's coral collections are at the University of Iowa,



Text-figure 23.—Correlation of the Cerro Gordo Member strata west to east, from Owen Grove to Rockford, Iowa. This is the source of much of the so-called "Hackberry" fauna, from outcrops at Hackberry Grove (type Lime Creek), Bird Hill, and at the Rockford Brick and Tile Company. Further information on localities is in the Appendix.

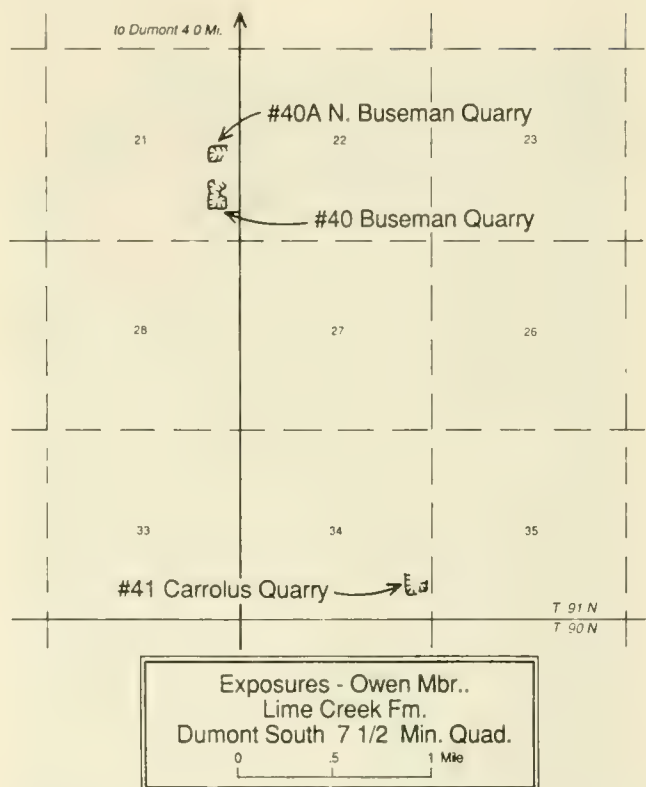


Text-figure 24.—Stratigraphic section showing correlation of beds within the Owen Member from the type locality at Owen Grove on the north to the Carrolus Quarry on the south. Localities are shown on Text-figs. 16, 25 and 26, and are described in the Appendix.



Text-figure 25.—Exposures of the Owen Member of the Lime Creek Formation in the Rockwell area, north of Sheffield, Iowa, in southernmost Cerro Gordo County. Exact geographic localities are shown; additional data is in the Appendix.

Iowa City (SUI). Specimens from Webster's private collection and some types from the present study are deposited at the Natural History Museum of the Smithsonian Institution in Washington, D.C. These have numbers referring to the United States National Museum (USNM). Several specimens referred to by Be-



Text-figure 26.—Location of three quarries in the Owen Member, located due south of Dumont, in Butler County, Iowa. Additional information is listed in the Appendix.

lanski (1928) are in the University of Cincinnati Museum (UCM). Additionally, some types and illustrated specimens have been deposited at the Paleontological Research Institution, Ithaca, New York (PRI).

SYSTEMATICS

Class **ANTHOZOA** Ehrenberg, 1834

Subclass **RUGOSA** Milne-Edwards and Haime, 1850

Order **STAURODIDA** Verrill, 1865

Suborder **KETOPHYLLINA** Zhyavoronkova, 1972

Family **ENDOPHYLLIDAE** Torley, 1933

The Family Endophyllidae is accepted here largely as defined by Hill (1981, p. F225), and the genus *Iowaphyllum* is placed therein, as was done by Hill. However, three genera also placed in this family by Hill are removed and placed in the Kyphophyllidae, as done by McLean and Pedder (1984, p. 18). These are the fasciculate genus *Smithiphyllum* and the solitary or sparsely colonial *Tabulophyllum* and *Tarphyphyllum*.



Text-figure 27.—Upper part of the Owen Member of the Lime Creek Formation at Carrolus Quarry, 1968 (Locality 41, Appendix). This photograph illustrates the alternating thick bedded and thin and rubbly bedded limestones of the upper Owen. The thinly bedded units contained numerous stromatoporoids and corals. As of 1989, the quarry is unused and flooded in great part.



Text-figure 28.—Complete sequence of the Owen Member of the Lime Creek Formation at the Buseman Quarry, south of Dumont, Iowa (Locality 40, Appendix). This photograph, taken in 1968 when quarry was being actively worked, illustrates the Owen, from approximately 1 ft (30 cm) above the Cerro Gordo to its top under the grass at the top of the picture. The uppermost limestones are of the "Acervularia" zone containing abundant colonial corals.

Genus **IOWAPHYLLUM** Stumm, 1949

Smithia Hall and Whitfield, 1873, p. 234 (not Milne-Edwards and Haime, 1851).

Strombodes Fenton and Fenton, 1924, p. 43.

Iowaphyllum Stumm, 1949, p. 50; Hill, 1956, p. F302; Stumm, 1964, p. 48; Strusz, 1967, p. 430; Oliver and Galle, 1971a, p. 213; Oliver and Galle, 1971b, p. 82; Coen-Aubert, 1974, p. 30; Fontaine, 1977, p. 473; Oliver, 1978, p. 799; Hill, 1981, p. F229; Sorauf, 1988, p. 166.

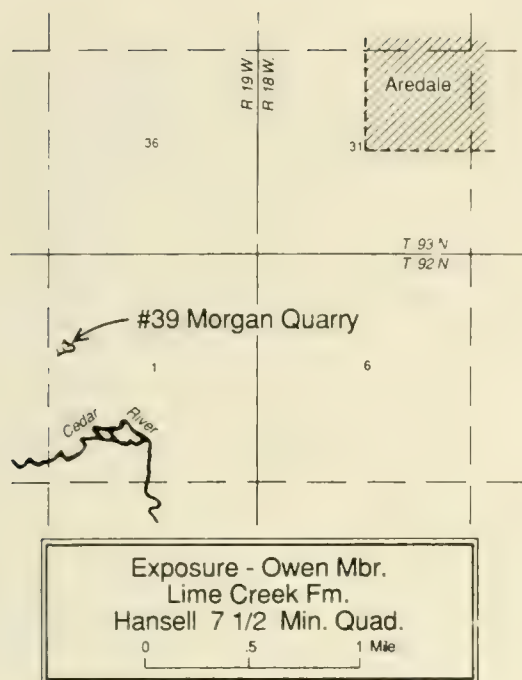
Type Species.—*Smithia johanni* Hall and Whitfield, 1873, original designation by Stumm (1949, p. 50).

Diagnosis.—Massive aphroid coralla, corallites with septa long and attenuate in tabularium and strongly dilated at margin of dissepimentarium. Septa then either 1) continue as dilated trabecular ridges to adjacent corallites as "septal crusts", or 2) die out as lonsdaleoid septa into areas of large and irregular dissepiments that separate corallites. Seen in longitudinal section, these conditions alternate in most coralla, so that septa are discontinuous in the dissepimentarium. Cor-

allites raised; thus, in planar transverse section aphroid appearance is emphasized. Tabulae divided into elevated axial and downwarped periaxial series. Wall-like surficial partitioning between corallites present in some species; likewise considerable variation in development of septal stereome between corallites.

Discussion.—Stumm (1949, p. 50) proposed the genus name for massive colonial corals with the type species *Smithia johanni* Hall and Whitfield, 1873. Stumm noted that septa could be in lateral contact across the wide dissepimentaria and that there was an apparent "repeated rejuvenescence" seen in longitudinal section. This "rejuvenescence" appears as vertically superposed zones of stereoplasm separated by zones of large dissepiments (see below) and probably reflects seasonal variation in skeletogenesis. Stumm included *Strombodes alpenensis* Rominger and *S. knotti* Davis in *Iowaphyllum*, along with *S. johanni*.

After descriptions of species by Fenton and Fenton



Text-figure 29.—Location of the Morgan Quarry (Owen Member). The quarry is in Franklin County, southwest of Aredale, Iowa. Additional information is found in the Appendix.

(1924) and the genus by Stumm (1949), these corals have been found over a wide geographic and stratigraphic range. Strusz (1967) described a species from Lower Devonian (Emsian) rocks of Australia and Oliver and Galle (1971a,b) recognized two Emsian species from Czechoslovakia. Fontaine (1977) described a Lower Devonian species from the north of France, and Coen-Aubert (1974) a Frasnian species from Belgium. Oliver (1978) described a species from Frasnian rocks of Arizona and presented a full discussion of the stratigraphic and geographic distribution of species within the genus. Sorauf (1988) recognized *I. johanni* in Frasnian strata of south-central New Mexico.

In addition to being important due to their geologic occurrence, these corals are interesting due to their singular structural features. As noted above, septa are vertically discontinuous except in the area directly adjacent to and within the tabularium, so that the appearance of the genus in longitudinal section is quite characteristic. Terminology for these septal elements is best borrowed from the cystiphyllids (McLean, 1976, p. 2) in which septal structures are described in terms of "crusts", composed of closely packed trabeculae on the surface of dissepiments. The crusts can split into rows of radially fused trabeculae referred to by McLean as "crests" that form ridges and may appear as septa in transverse section. *Iowaphyllum* thus has crusts occurring periodically, in longitudinal section

Table 2.—Stratigraphic distribution of species of rugose corals within the Shell Rock and Lime Creek Formations of north central Iowa. The subdivisions shown at the right are as follows: for the Shell Rock Formation are (1) the Mason City Member, and (2) the Nora Member; subdivisions of the Lime Creek are (3) the Cerro Gordo Member, and (4) the Owen Member.

Biostratigraphy	Shell Rock		Lime Creek	
	1	2	3	4
<i>Smithiphyllum belanskii</i>	X			
<i>Pachyphyllum websteri</i>	X			
<i>Tabulophyllum mutabile</i>	X			
<i>Tabulophyllum curtum</i>	X			
<i>Disphyllum floydense</i>	X			
<i>Disphyllum iowensis</i>	X			
<i>Pachyphyllum minutissima</i>	X			
<i>Trapezophyllum</i> sp.	X			
<i>Tabulophyllum buccinum</i>		X		
<i>Tabulophyllum</i> n.sp. A		X		
<i>Tabulophyllum</i> n.sp. B		X		
<i>Tarphyphyllum cylindricum</i>		X		
<i>Disphyllum conjugans</i>		X		
<i>Macgeea concinnula</i>		X		
<i>Tarphyphyllum</i> sp.		X		
<i>Hexagonaria oweni</i>		X		
<i>Pachyphyllum gregarium</i>		X		
<i>Iowaphyllum johanni</i>			X	
<i>Tabulophyllum rectum</i>			X	
<i>Tabulophyllum ehlersi</i>			X	
<i>Tabulophyllum rotundum</i>			X	
<i>Tabulophyllum ellipticum</i>			X	
<i>Tabulophyllum ponderosum</i>			X	
<i>Tabulophyllum robustum</i>			X	
<i>Charactophyllum nanum</i>			X	
<i>Disphyllum dispassum</i>			X	
<i>Hexagonaria inequalis</i>			X	
<i>Pachyphyllum woodmani</i>			X	
<i>Macgeea solitaria</i>			X	
<i>Disphyllum</i> sp.				X
<i>Hexagonaria bassleri</i>				X
<i>Tabulophyllum longum</i>				X
<i>Tabulophyllum magnum</i>				X
<i>Tabulophyllum expansum</i>				X
<i>Pachyphyllum dumonti</i>				X
<i>Pachyphyllum crassicostatum</i>				X
<i>Macgeea camplanulata</i>				X

separated in vertical sequence by layers of dissepiments that are commonly large and globose; these crusts are vertically continuous and form septa only in the area directly around and within the tabularium. Seen in transverse sections, *Iowaphyllum* generally appears to be aphroid, as recognizable septal "crests" adjacent to tabularia are not continuous from one corallite to another. Since corallite tabularia tend to be elevated, part of the apparent aphroid nature of septa is due to intersection of a curving plane of septal crusts by a flat thin section. Seen in longitudinal section, crusts are commonly, although not always, continuous from one corallite to another. Thus the term "aphroid"

applied to *Iowaphyllum*, has a slightly different meaning than when applied to genera with more typical, fully formed septa. Some specimens of *Iowaphyllum* are also aphroid in the usual sense, with crusts not continuing from one corallite to the next.

A number of methods exist for differentiating between species of *Iowaphyllum* within a sample such as that collected from the Lime Creek Formation. All specimens have been collected from the same horizon within the Cerro Gordo Member, from a silty limestone that weathers iron-stained and exhibits extensive burrowing in its upper part. Literature on the genus, and on colonial corals in general, suggests that a list of criteria for species differentiation would include the following (listed from most generally used to most specific to this genus):

1. diameter of tabularium,
2. number of septa,
3. distance between corallites, measured from axis to axis,
4. presence and amount of stereome within corallum,
5. presence of elevated margins around tabularia, and
6. presence of a ridge serving to separate corallites, thus acting as a temporary corallite wall.

Criteria are here reviewed from the bottom upwards. The presence or absence of a ridge forming a "wall", a polygonal margin to individual corallites on the oral surface, is a variable phenomenon within the Iowa fauna. It is noted in many specimens of *I. johanni*, including a weak but persistent development in the holotype. The feature is seen in longitudinal sections of the species, particularly occurring in those colonies that appear to contain abundant and widespread stereome in transverse section. This seems to be related to the development of thick, crested ("septate") stereome mats between corallites. The development of this stereome apparently favors structural partitioning of corallites by ridge formation. The occurrence of the two features (stereome mats and ridges) is nearly random in the Lime Creek fauna, and does not suffice to differentiate species in this fauna. Where consistently and prominently developed, as in *Iowaphyllum nisbeti* Oliver, 1978, the character does serve to define a species.

That part of the corallite immediately surrounding the tabularium in *Iowaphyllum* is generally elevated somewhat above the rest of the corallite surface. Well-developed relief of this type led Hall and Whitfield to erect the species *Smithia multiradiata*, and the development of distinct, wall-like ridges surrounding corallites led Fenton and Fenton to propose the species

Strombodes marginatus. The two species, as originally proposed, were based on characters observable on free-weathered corallite surfaces, and there is considerable variation in these features in the two holotypes. In the Lime Creek fauna collected for this study, many specimens have come from the "rusty bed" of the Cerro Gordo Member, with a maximum outcrop separation of less than 10 km (6 mi.). The presence and form of the peri-tabular boss varies within this local fauna and apparently does not correlate with other characters.

The amount of stereome within coralla permits grouping specimens. Stereome occurs as mat-like, inflated, laterally coalesced septal crusts that are sometimes confluent between tabularia. Since these mats are vertically discontinuous, care must be taken to compare thin sections taken from equivalent positions within colonies, as sections taken between layers of stereome show large dissepiments dominating areas between corallites. However, regardless of position of section, *I. johanni* still contains some colonies with little stereome, and some with very widespread and thick deposits of septate stereome. I consider this to be variation of colonies within the one species.

Distance measured from corallite axis to that of each neighboring corallite within colonies has been used to differentiate species of *Iowaphyllum* by Oliver (1979, p. 799). Measurements by me indicate that there is a marked effect on measured distances by position with respect to growth of the colony. Distance between corallites varies as colony shape varies, and also varies with corallite position within the colony between means derived from corallites in central positions within a colony and means derived from peripheral corallites in the same colony. Extreme care must be used when comparing these mean distances between colonies.

The number of septa is a useful character for species discrimination. In *Iowaphyllum*, the number of septa in a corallite correlates to the diameter of the corallite, with larger diameter corallites accommodating larger numbers of septa. There does seem to be a characteristic mean number of septa for each species.

Diameter of corallites is a basic character used in speciation. In the Lime Creek fauna, *Iowaphyllum* is differentiated into two groups, one of which has consistently larger corallite diameters. The absence of other characters allowing differentiation of species consistent with those based on size suggests to me that the differences are not of specific rank. The two sizes are here regarded as variants of *Iowaphyllum johanni*, and names should not be given to them.

Distribution.—*Iowaphyllum* occurs in Lower or Middle Devonian strata of Australia, the Bohemian

massif, and occurs widely in Frasnian rocks of North America and Europe. It is known from Arizona, New Mexico and Iowa in North America and from the Ardennes and Rhenish Massif in Europe.

***Iowaphyllum johanni* (Hall and Whitfield, 1873)**

Plate 2, figures 6,7; Plate 4, figures 1–7; Plate 5, figures 1–6; Plate 6, figures 1–3

Smithia johanni Hall and Whitfield, 1873, p. 234, Pl. 9, fig. 10.

Smithia multiradiata Hall and Whitfield, 1873, p. 234.

Strombodes johanni Fenton and Fenton, 1924, p. 43, Pl. 15, figs. 6–7.

Strombodes johanni multiradiata Fenton and Fenton, 1924, p. 44, Pl. 15, fig. 1.

Strombodes marginata Fenton and Fenton, 1924, p. 44, Pl. 15, figs. 2–5.

Iowaphyllum johanni Stumm, 1949, p. 50, Pl. 25, figs. 1–5; Oliver and Galle, 1971a, p. 212, Pl. 4, figs. 1–4; Sorauf, 1988, p. 166, figs. 12.3–12.6, 14.1–14.3; McLean and Sorauf, 1989, p. 395, figs. 1,2.

Iowaphyllum sp. cf. *I. johanni* Oliver, 1978, p. 800, figs. 4a-b.

Diagnosis.—Species of *Iowaphyllum* with variable calicinal features, namely, amount of stereome present as septal crusts, size of tabularium and distance between corallites. Colony mean diameter of tabularium varies from 15 to 19 mm. Septal crusts may be only sporadically present, or developed so that more than 75% of surface area is stereome in transverse section. Dissepiments generally low and flattened but can be extremely large and irregularly bulbous where stereome is lacking; only two or three dissepiments separate tabularia of neighboring corallites.

Description.—On weathered calicinal surfaces of colonies, septal crests are commonly seen on the stereome crust, thus superficially resembling thamnasterioid colonies, with crests confluent from one corallite to the next. A weak ridge sometimes forms where an intercorallite wall would occur. The surface prominence of the area surrounding the tabularium often is little developed in this species, being only 1–2 mm high in the holotype of *I. johanni*, only $\frac{1}{3}$ the height described in *Strombodes marginatus* by Fenton and Fenton (1924, p. 44).

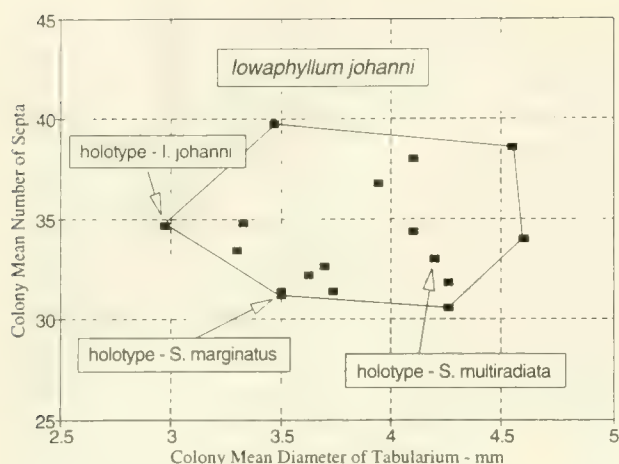
In transverse thin sections of typical *I. johanni*, major septa are long, reaching to the axis of the corallite and joining in an irregular fashion. Minor septa are short; generally the tabularium is completely ringed by solid stereome without extension of minor septa into the tabularium. In intercorallite spaces, septal crests are much in evidence as lines of trabeculae within crusts composed of stereome and trabeculae. In the holotype, there is considerable development of septate crests around each corallite, with only $\frac{1}{3}$ to $\frac{1}{4}$ of total intercorallite space occupied by dissepiments of various sizes and shapes (Pl.4, fig.1). Several corallites are completely joined by these septal crests.

In longitudinal section, the tabularium shows distinct axial and periaxial series of tabulae, with the axial row arched in the adoral direction. In the dissepimentarium (which is coextensive with the intercorallite space or coenosteum) episodic development of septa is well-displayed, with septal crests formed of vertically directed trabeculae. The stereome surface is perpendicular to the trabeculae (Pl.4, figs.2,6). The episodic (perhaps periodic) development of these septate mats of stereome was referred to as “repeated rejuvenescence” by Stumm (1949, p. 50). Arching of the upper surface of crests near the tabularium leads to a very slight divergence of trabeculae. The dissepiments between septal crusts are irregular in size and number, comprising a layer, generally of four to seven rows, separating neighboring tabularia. The term “aphroid” is not totally appropriate to describe the appearance of this colony, as septal crests are continuous between tabularia. The rise in the surface of the crust near a tabularium results in the more common appearance of septal crust near tabularia in a planar thin section, and the crust may not be visible farther out in the dissepimentarium.

Type Specimens.—Holotype NYSM 3720/1; the label notes that the specimen was collected from “marly beds at Hackberry, eight miles above Rockford, Iowa” (Hall and Whitfield, 1873, p. 234). This is Locality 28 of the present study (see Appendix). *Smithia multiradiata* holotype is NYSM 3721/1. *Strombodes marginatus* holotype is FMNH 26053, paratype is UMMP 8087.

Discussion.—It is convenient to recognize within the Iowa fauna two forms, here informally called the *johanni* and *multiradiata* groups. I separate the two on the basis of the colony mean diameter for the tabularium, with *johanni* s.s. being characterized by a consistently smaller diameter of tabularium (with a mean ranging from 2.9 to 3.8 mm (Text-fig. 30). The holotype of the species has a colony mean of 2.9 mm. Those corals referred to as the *multiradiata* group are somewhat larger, with mean tabularial diameters ranging from 3.9 to 4.6 mm per colony. The size ranges form a continuum.

Within *I. johanni*, groups of colonies illustrate the variation present within the species. At one end of the scale of variation are a number of colonies marked by the standard size tabularium (for the form), with minor amounts of stereome occurring as septal crusts (Pl.4, fig.4), and a wide dissepimentarium which may have very large dissepiments (Pl.4, fig.5). This is characteristic of the holotype of *Strombodes marginatus* Fenton and Fenton (Pl.4, fig.5; Pl.5, fig.5). The large, bulbous dissepiments are quite characteristic of this subgroup, which grades into a second, with large dissepiments



Text-figure 30.—*lowaphyllum johanni*, from the Cerro Gordo Member, colony mean diameters (in mm) plotted versus the colony mean number of total septa (major and minor). The holotype colonies of *Strombodes marginatus* Fenton and Fenton and *Smithia multiradiata* Hall and Whitfield are also shown on this graph.

and a standard size tabularium, but with septal crusts (stereome) much more obvious in transverse section (Pl.5, fig.6).

A third group of these colonies includes those with standard tabularium diameter, but with the heavy development of septal crusts (Pl.5, fig.2). In longitudinal section, these corals generally do not show elevated margins around the tabularia, but may in some cases show weak development of the "wall-like" ridge marking what would be the boundary of individuals. The holotype of *I. johanni* has such ridges weakly developed. They are observable on the weathered calicinal surface and occasionally in thin section. The feature is better developed in some other specimens where it can be seen in transverse thin sections as straight-line margins to areas of stereome and as discontinuous vertical prominences in longitudinal section (Pl. 5, figs.2,3; Pl.6, fig.3). These ridges are never as continuously or fully developed here as in *I. nisbeti* Oliver, from Frasnian rocks in Arizona (Oliver, 1978, p. 799). One paratype specimen (UMMP 8086) of *Strombodes marginatus* Fenton and Fenton also belongs in this third grouping, as it is characterized by a high prominence surrounding the margin of the tabularium and a weak wall-like ridge.

The *I. multiradiata* group shows a similar pattern of variation, but is characterized by larger tabularial diameters. There are two intergradational clusters, one characterized by a general lack of stereome, with dissepiments that are extremely large and irregular (Pl.5, fig.5), and a second, also with a similarly large tabularium, but with fuller development of septal crusts. A prominence is variably developed around the margin

of the tabularium, but where developed, tends to be smoothly rounded, rather than being somewhat abrupt as in *I. johanni* s.s. This last includes the holotype of *Smithia multiradiata* Hall and Whitfield (NYSM 317), and also one of the paratypes of *Strombodes marginatus* Fenton and Fenton (UMMP 8087).

To summarize the preceding: 1) there does not seem to be a straightforward way to divide this fauna into more than one species, and 2) although specimens can generally be placed in the one group or the other by the average size of their corallites, this is within a size continuum. Each size group shows parallel change from forms with large irregular dissepiments and weakly developed septal crusts to colonies with heavier septal crusts and sometimes with elevated margins around the tabularium as well as the weak development in some specimens of a wall-like ridge from the septal crust. Thus, I place the species *Smithia multiradiata* Hall and Whitfield, 1873, and *Strombodes marginatus* Fenton and Fenton, 1924, into synonymy with *lowaphyllum johanni* (Hall and Whitfield, 1873).

Smithia multiradiata corallites are characterized by a distinct, smoothly rounded prominence centered on the tabularium. The feature is well shown in the holotype (NYSM 3721/1; Pl.4, fig.3). As noted previously, the calicinal boss surrounding the tabularium is variable within *lowaphyllum johanni*, and the holotype of *I. multiradiata* is similar in all ways to other typical specimens of *I. johanni* that have heavy development of septal crusts but lack wall-like ridges (Pl.5, fig.6). The tabularial diameters in the holotype of *S. multiradiata* are larger than typical, with a mean of 4.2 mm, but, as discussed above, this occurs within the continuous size variation of *I. johanni*.

Strombodes marginatus was proposed by Fenton and Fenton (1924, p. 44), on the basis of the presence of calicinal bosses centered on the tabularia, with the "area about the depression sharply elevated, in some specimens as much as 2.5 mm above the general surface of the corallite, which is convex", and with septa that are "strongly flexuous and are elevated at the periphery to form distance boundaries for the corallites" (1924, p. 45). None of these coral colonies were thin-sectioned until the present study. The holotype (FMNH 26053) is a typical member of the *I. johanni* species group, characterized by light development of septal crusts, a small mean size of tabularial diameter (3.74 mm), and a sharply raised rim around the tabularium, but with no development of a wall-like ridge between corallites. The two paratypes vary in size, one with small tabularial diameters (mean, 3.5 mm, UMMP 8086) and the other large (mean, 4.55 mm, UMMP 8087). Each has an elevated area around the margin of the tabularium, and each shows the weak

development of a wall-like ridge between some corallites. The ridge here is little more developed than in the holotype of *I. johanni*. The species *I. marginatus* is a synonym of *I. johanni*.

Iowaphyllum johanni has also been reported from the Martin Limestone (Frasnian) of Arizona by Oliver (1978, p. 800), who briefly described and illustrated his specimen as *I. sp. cf. I. johanni*, which I accept as *I. johanni*. It is also common in the Sly Gap Formation (Frasnian) of south central New Mexico (Sorauf, 1988, p. 166).

Occurrence.—Fenton and Fenton (1924, p. 43) noted that *Iowaphyllum johanni* occurs in the "Upper portions of the *Spirifer* zone and the Owen". They also stated that their species, *Strombodes marginatus*, here regarded as synonymous with the former, likewise occurs in "Upper portions of the *Spirifer* zone and probably in the Owen. It is especially characteristic of the *Stromatoporella* faunule at Hackberry Grove" (1924, p. 45). All specimens from Fenton collections at UMMP and FMNH are labeled as coming from the "*Spirifer* zone" at Hackberry Grove (Locality 28 of this study, Appendix). My experience is that all specimens of *Iowaphyllum* occur in a single bed, the "rusty bed" of the medial Cerro Gordo Member, in which they are found with abundant stromatoporoids, the rugosans *Hexagonaria inaequalis*, and *Pachyphyllum woodmani*, as well as the tabulate *Alveolites rockfordensis*. This is also the only level at which the stromatoporoids and this species of *Hexagonaria* are found. Approximately 20 colonies of *Iowaphyllum* were noted, always in this bed, at South Portland (Localities 27 and 27a, Appendix) and from type Lime Creek strata (Locality 28). In 1986, the best place to collect abundant *Iowaphyllum* was at Locality 28B, Lime Creek East, where annual plowing of a corn field exposes many colonial corals from this level of the Cerro Gordo Member. Most certainly the species does not extend into Owen beds.

Family KYPHOPHYLLIDAE Wedekind, 1927

The Kyphophyllidae, as discussed by McLean and Pedder (1984, p. 18), includes genera characterized by very fine septal trabeculae, vertically elongate dissepiments and presepiments, and a distinctive tabularium with flat or arched tabulae. Among others, these authors included the genera *Tabulophyllum*, *Tarphyphyllum*, and *Smithiphyllum*, all of which occur in the Iowa Frasnian. I adopt their concept of the family, finding that these genera have much in common.

Hill (1981, p. F223) previously defined the family quite differently from McLean and Pedder. She regarded the family as containing genera with small, multiserial septal trabeculae. In other criteria, the fam-

ily as she defined it could contain *Smithiphyllum* and *Tabulophyllum*.

Genus TABULOPHYLLUM

Fenton and Fenton, 1924

- Chonophyllum* Hall and Whitfield, 1873, p. 233; Fenton and Fenton, 1924, p. 29.
Tabulophyllum Fenton and Fenton 1924, p. 30; Stumm, 1940, p. 60; Smith, 1945, p. 58; Stainbrook, 1946, p. 416; Stumm, 1949, p. 27; Soshkina, 1951, p. 34; Bulvanker, 1958, p. 162; Watkins, 1959, p. 81; (part) Soshkina, 1960, p. 290; Spassky, 1960, p. 25; Pitrat, 1962, p. 1159; Stumm, 1962b, p. 292; Soshkina, Dobrolyobova, and Kabakovich, 1962, p. 342; Ivania, 1965, p. 24; Tsien 1969, p. 37; Hill and Jell, 1970, p. 63; Tsien, 1976, p. 266; Spassky, 1977, p. 115; Birenheide, 1978, p. 64; Rozkowska, 1980, p. 42; (part) Onoprienko, 1979, p. 29; Hill, 1981, p. F229; Coen-Aubert, 1982, p. 37; Sorauf, 1987a, p. 16; 1987b, p. 677; 1988, p. 158; 1989, p. 397.
Apolythophyllum Walther, 1928, p. 135.
?Sinospogonophyllum Yoh, 1937, p. 56; Hill, 1942, p. 20; Fontaine, 1966, p. 62; Strusz, 1967, p. 431.
Eurekaphyllum Stumm, 1937, p. 431; Stumm, 1949, p. 17.
Diversophyllum Sloss, 1939, p. 65; Stumm, 1940, p. 58; 1949, p. 25.

Type Species.—*Tabulophyllum rectum* Fenton and Fenton, 1924, p. 31.

Diagnosis.—Solitary kyphophyllid corals of variable size (small to large) characterized by amplexoid septa in two orders. Major septa commonly long, extending to near axis of corallite, but generally leaving open axial space, which lacks an axial structure. Minor septa always short, commonly discontinuous in dissepimentarium, only short spines in some species. Lonsdaleoid dissepimentarium present to variable extent in all species, with presepiments interrupting septa in outer dissepimentarium. Tabulae commonly complete and flat in tabularium, with peripheral sag causing gutter-like structure. Septa with fine monacanth trabeculae. Corals substrate adaptive, with prominent talons developed on hard substrate and multiple thin, leaf-like presepiments formed on very soft substrates.

Discussion.—*Tabulophyllum* was established by Fenton and Fenton in 1924, with *Tabulophyllum rectum* the type species. The species, as here defined, is more inclusive than as described by Fenton and Fenton, who based species descriptions narrowly, on features that commonly change as ecological adaptations.

In general, the genus comprises two groups of species, one with medium to small corallite diameters and the other with large diameters. The former tend to be somewhat generalized corals without marked symmetry or specialized structures, but with great variation in form according to ecologic circumstances, as in *Tabulophyllum rectum*. The latter tend to develop bilateral symmetry, a shortened cardinal septum, and differential septal dilation in the cardinal quadrants. The

latter are typified by the species *Tabulophyllum longum* and *T. magnum* of the Owen Member of the Lime Creek Formation, both of which are large and vary from corallites with no bilaterality to individuals with it well-developed and often accompanied by shortening of the cardinal septum. When septa are long, these large corals may have an axial boss formed by swirling of septa around the corallite axis.

The microstructure of septa and tabulae is finely trabecular and fibronormal when best preserved (Sorauf, 1989, p. 401). The corallite wall is a septotheca formed of the expanded and coalesced bases of septa, composed of fibrous crystallites, but commonly modified into a secondarily lamellar wall structure by diagenesis (Sorauf, 1996, p. 69).

Species of *Tabulophyllum* also show apparent adaptations to differing substrates, as follows: apical talons developed, probably to form a wide base on hard substrate; leaf-like presepiments developed, possibly to provide stability on, or in, very soft substrates; and there is a suggestion that secondary calcite deposited in the apices of corallites may have provided added stability in shifting substrates. Several of these possibilities are discussed below in species descriptions.

All authors are agreed that *Apolythophyllum* Walther, 1928 is a synonym of *Tabulophyllum*, following the lead of Lang *et al.* (1940, p. 18). This agrees with Hill (1981, p. F229). *Diversophyllum* Sloss, 1939 is also a synonym of *Tabulophyllum*, although Sloss (1939, p. 66) regarded it as separate because of what he termed "definite and persistent minor septa". Watkins (1959, p. 82), studied material from Middle Devonian beds in Michigan, and concluded that the two genera are similar internally and thus regarded them as synonyms. I have studied numerous topotypes of *Diversophyllum traversense*, type species of the Sloss genus, and regard them as *Tabulophyllum* without question. Minor septa are no more continuous in this species than in typical *Tabulophyllum*. Hill (1981, p. F230) placed this genus into synonymy with *Tabulophyllum* with a query, which is unnecessary.

Sinospongophyllum Yoh, 1937 was established for solitary corals with flat tabulae and an "inner wall" which separated the lonsdaleoid part of the corallite from the inner (Yoh, 1937, p. 56). Wang (1948, p. 31) noted that the type species, *S. planotabulatum*, contains mostly solitary corals, but that the species is "sometimes weakly compound". Wang here authored two other species that are strictly solitary. Uncertainty regarding the possibly colonial nature of *Sinospongophyllum* is the only reason for querying the placement of this genus as a synonym of *Tabulophyllum*, as has Hill (1981, p. F230). It should be synonymized if *S. planotabulatum* is only occasionally compound, as nu-

merous solitary genera of the Rugosa occasionally bud. Soshkina (1951) and Bulvanker (1958) both have included colonial species in *Tabulophyllum*, *T. weberi* by the former, and *T. sibericum*, *T. butovi* and *T. schliiteri* by the latter. This is an unacceptable change in the genus concept based on the Iowa fauna.

Distribution.—The geologic range of *Tabulophyllum* is from the Pragian, in the Mt. Etna Limestone of Queensland (Strusz, 1972, p. 447) to questionably early Famennian and very questionably late Famennian. Although Hill (1942, p. 20) described the early species as *Sinospongophyllum abrogatum*, she noted that the genus might be identical to *Tabulophyllum*. Species of *Tabulophyllum* are abundant in highest Lower Devonian strata of Europe (Tsien, 1969) and are present and characteristic worldwide in Middle and lower Upper Devonian rocks. The cosmopolitan Frasnian faunas are similar worldwide to those of Iowa.

Reported Famennian occurrences of the genus can be discounted in part. The report of *Tabulophyllum maria* from early Famennian rocks of Moravia in the Czech Republic (Galle, 1987) however, is apparently valid (depending on dating of strata); this and a possible Famennian occurrence of *T. gorskyi* in Poland (Rozkowska, 1969) would mean that species of this genus survived the late Frasnian extinction event. It appears unlikely that late Famennian (Strunian) species are properly placed in this genus (Onoprienko, 1979; Poty and Onoprienko, 1984). No Lower Carboniferous species are referable to *Tabulophyllum*, although Soshkina (1960) argued otherwise. Further discussion is presented in Sorauf (1989).

***Tabulophyllum rectum* Fenton and Fenton, 1924**

Plate 1, figure 9; Plate 6, figures 4–10; Plate 7, figures 1–5

Tabulophyllum rectum Fenton and Fenton, 1924, p. 30, Pl. 6, figs. 8–12; Smith, 1945, p. 58, Pl. 2, figs. 10, 11; Pl. 3, fig. 8; Stumm, 1949, p. 69, fig. 18; Hill, 1956, p. F300, fig. 205.c,d; Watkins, 1959, p. 81, Pl. 16, figs. 10–12; Hill, 1981, p. F229, figs. 2a,b; Sorauf, 1989, p. 402, figs. 1–4.

Tabulophyllum regulare Fenton and Fenton, 1924, p. 33, Pl. 6, figs. 1, 2.

Tabulophyllum erraticum Fenton and Fenton, 1924, p. 36, Pl. 6, figs. 3–7.

Diagnosis.—Small species of *Tabulophyllum* with 30 to 35 major septa and discontinuous minor septa developed as septal spines. Attenuate major septa reach near axis but do not unite or form axial structure. Lonsdaleoid dissepimentarium variably developed, commonly narrow, but expands and contracts regularly. Tabulae commonly complete, forming flat, raised platform throughout most of tabularium, with peripheral trough formed of downbent edges of tabulae.

Description.—*Tabulophyllum rectum*, type species

of the genus, is small and is rounded to slightly ovoid in outline, generally with a trochoid or irregularly elongate ceratoid form (Pl.1, fig.9). The diameter is 13 to 18 mm; the holotype has a total diameter of 16 mm, and its tabularium diameter is 14 mm. Major septa are attenuate and long, reaching into the axial area, although not extending to the axis. Septa are thin throughout the corallite and are only continuous within the tabularium. Minor septa are poorly developed (Pl.7, figs.2,3,4), occurring as spines in the peripheral part of the dissepimentarium, or occasionally as spines with a wedge-shaped base in the septotheca. Presepiments are elongate (Pl.6, figs.4,6), and generally continuous, interrupting both major and minor septa. The dissepimentarium is seen expanding and contracting in longitudinal section, commonly with an asymmetry in which one side contains larger and more bulbous presepiments and expands and contracts more than the other side, as in the longitudinal section of the holotype. In longitudinal view tabulae tend to be complete and flat, with a sinusoidal sag at the periphery of the tabularium. The tabularium is highly variable, ranging from one with evenly spaced complete tabulae to one with growth bands of bunched tabulae, which are less complete where closely spaced. Where very regular, these are segregated into growth bands that are uniformly composed of flat-topped, incomplete tabulae (as in *T. regulare* Fenton and Fenton, 1924, p. 33). Where irregular growth has occurred, the tabulae and tabularium reflect this, with widely spaced, sloping, complete tabulae (Pl.6, fig.9) formed at times of rapid growth and more typical and regular tabulae during times of slower growth (e.g., holotype of *T. erraticum* Fenton and Fenton, 1924, p. 36). Irregular growth is likewise shown by contraction and expansion of the dissepimentarium, apparently reflecting the response of a polyp to changing environmental conditions.

The external form of the species is variable, with the shape seemingly controlled by environment, in part resulting from direction of growth and in part controlled by expansion and contraction of the dissepimentarium, and at the extreme resulting in laterally extended, large, leaf-like presepiments which may have aided in positioning the coral and maintaining a somewhat erect position for the polyp above the sediment-water interface (Pl.6, fig.8). This variability has led to confusion and the multiplication of species names.

Type Specimens.—Holotype UMMP 7834, paratypes UMMP 7835, 7836, 7827 and FMNH 26046. *T. regulare* holotype UMMP 7824, paratype UMMP 7825. *T. erraticum* holotype FMNH 26006, paratypes UMMP 7823, 7822, 7841, 7794, 7795, and 7796.

Discussion.—The species *Tabulophyllum rectum*

from the Lime Creek Formation is a variable form which encompasses the holotypes of *Tabulophyllum regulare* and *T. erraticum*, both described by Fenton and Fenton and partly based on growth characters. Thus, *T. rectum* had a straight (erect) form with a pole as a growth axis, *T. erraticum* had a twisting, erratic growth form, and *T. regulare* had regular expansions and contractions of the dissepimentarium coupled with regular development of bands of closely spaced tabulae. Providing these characters were a response to changing living conditions, forms with very regular growth thus were most likely living on a sea floor with constant rate of sedimentation, while forms with erratic growth forms likely reflect episodic toppling of corals by currents at the sediment-water interface. The presence of large presepiments in this species possibly served a support function in and on soft substrate.

Tabulophyllum rotundum Fenton and Fenton, 1924 is very similar to *T. rectum* except that it has abundant and prominent presepiments. The completeness and regular development of the lonsdaleoid dissepimentarium in *T. rotundum* warrants retention of the separate species name. It is also possible, however, that this is a variant of *T. rectum*, with the species thus having a morphotype with abundant, large dissepiments as an adaptation for life on soft substrate.

Occurrence.—*Tabulophyllum rectum* occurs in the “*Spirifer* zone, and *Idiostroma* zone of the Owen”, according to Fenton and Fenton (1924, p. 32). *T. regulare* and *T. erraticum* likewise are found in the “*Spirifer* zone”, with the former also “perhaps in the lower portions of the Owen” (p. 34). My experience is that the species *T. rectum* does not occur above or below the “*Spirifer* zone” of the upper Cerro Gordo Member. Numerous specimens were collected from various parts of this unit at the following: Type Lime Creek (Locality 28, Appendix), Bird Hill North (Locality 30), Bird Hill (Locality 31), Bird Hill South (Locality 32), and at the Rockford Brick and Tile Company Quarry (Locality 35).

***Tabulophyllum ehlersi* Fenton and Fenton, 1924**
Plate 1, figure 10; Plate 7, figures 6–16

Tabulophyllum ehlersi Fenton and Fenton, 1924, p. 34, Pl. 6, figs. 12–16; Smith, 1945, p. 61, Pl.3, figs. 9,10.

Diagnosis.—Small species of *Tabulophyllum* characterized by elliptical to elongate, compressed transverse outline and development of prominent talons.

Description.—Small (maximum diameter approaches 3 cm), oval solitary corals characterized by prominent talons and broad, elongate attachment base. Septa are in two orders with minor septa generally only developed as wedge-like ridges on the external wall and

on the first heavy presepiment in from the wall. Major septa are amplexoid and may be long, continuous and attenuate; they extend into the tabularium and swirl around an open axis (Pl.7, fig.11), or are incomplete and long, extending to axis only on tabulae, but not touching one another. There are 30 to 38 major septa in the eight specimens examined. Maximum diameters range from 24 to 31 mm. The mean number of major septa is 34.8, thus the mean total number of septa for *T. ehlersi* is nearly 70. Major septa are generally discontinuous in the lonsdaleoid dissepimentarium, broken by prominent presepiments. In transverse sections, *T. ehlersi* commonly has a prominent presepiment which rivals the epithecal wall in thickness (Pl.7, figs.10,11). Both commonly have the wavy lamellar (diagenetic) microstructure that is widespread in specimens of other species of this genus.

In longitudinal section, cut parallel to the axis of elongation, the interior is dominated by long, generally complete tabulae. In the axial region the tabulae form a flat-topped arch and a peripheral trough in the outermost tabularium (Pl.7, fig.13). Dissepiments are variably developed, at the most forming a dissepimentarium with two to four rows of large, steeply inclined dissepiments. It is common, however, to have only one row of very large, nearly vertical dissepiments. Presepiments tend to be more robust than others and are commonly sediment-filled. The presence of a pedestal formed by talons on hard substrates appears in longitudinal section as a lateral outgrowth of tabulae and dissepiments, with growth preferentially along the long axis of the elliptical corallite (Pl.7, figs 15,16). Amplexoid septa are fixed at their base to the top of flat, complete tabulae.

Type Specimens.—Holotype UMMP 7815; paratypes UMMP 7816–7821.

Discussion.—*Tabulophyllum ehlersi* has not been reported from any area other than Iowa, nor are other elliptical species of *Tabulophyllum* known anywhere, with the exception of the large *Tabulophyllum ellipticum* (Hall and Whitfield, 1873, p. 233) from the Lime Creek Formation.

In their study of the Lime Creek fauna, Fenton and Fenton undoubtedly relied too much on external morphology of the corals. The development of an ovate form is seen in some life stages of *T. rectum*, and may approach the cross-section dimensions of *T. ehlersi*. In the latter, the shape is consistent and warrants retaining the species name. No small species of the genus have been reported from Frasnian strata elsewhere (or of other ages) with a consistent elliptical cross sectional outline, as here developed in *T. ehlersi*.

Occurrence.—Specimens of *T. ehlersi* were collected from the upper part of the "Spirifer zone" of the

Cerro Gordo Member at the following localities: South Portland (Locality 27), Type Lime Creek (Locality 28), Bird Hill (Locality 31), Bird Hill South (Locality 32), Juniper Hill (Locality 34) and the Rockford Brick and Tile Company Quarry (Locality 35). Fenton and Fenton also stated that it occurs in the lower part of the Owen Member (1924, p. 35). I have not seen specimens from the Owen, either in the field or in museum collections and I assume that the report is erroneous.

***Tabulophyllum rotundum* Fenton and Fenton, 1924**
Plate 8, figures 1–16; Plate 9, figures 1–3

Tabulophyllum rotundum Fenton and Fenton, 1924, p. 35, Pl. 2, figs. 5–10; Sorauf, 1989, p. 402, Pl. 1, figs. 5–8, 13–16.
Tabulophyllum sylvaticum Rohart, 1988, p. 244, Pl.29, figs. 4,5.
not *Tabulophyllum rotundum* Spassky, 1960, p. 26, Pl. 1, figs. 3,4, Pl. 2, figs. 1–6, Pl. 3, figs. 1,2.

Diagnosis.—Small- to medium-sized, ceratoid to trochoid *Tabulophyllum* with continuous and volumetrically important lonsdaleoid dissepimentarium. Radially arranged amplexoid, attenuate septa reach into tabularium, with flat, generally complete tabulae and prominent, widely-flaring presepiments.

Description.—*T. rotundum* comprises small to medium corals with diameters of from 15 to 20 mm, and lengths of from 30 to 50 mm, with the more elongate ceratoid forms approaching 50 mm, the maximum length. Shorter, trochoid corals generally flare somewhat in the calicinal end, with a deep and flat-bottomed calice. Diameter in mature part of corallites ranges from 19 to 23 mm in seven specimens studied (mean of 21 mm). Radial, amplexoid septa are in two orders, with 30 to 35 major septa generally long and attenuate; they invariably reach into the tabularium, and sometimes extend discontinuously to the axis of the coral. Most commonly, an open space is left at the axis. The lonsdaleoid dissepimentarium is always a prominent part of corallite in this species, with the outer portion of the dissepimentarium characterized by large and heavy presepiments, each of which functioned as a wall, barring sediment from the central portion of the coral and bearing both major and short minor septa (Pl.8, figs.3,10,12).

Longitudinal sections are characterized by complete tabulae that are adorally arched with a flat top in the axial portion of the coral and with a peripheral trough around the outer tabularium (Pl.8, figs.1,4). Amplexoid septa have their bases rooted on tabulae. Occasional tabulae reach very great size and are continuous into the dissepimentarium (Pl.8, fig.6). Dissepiments are elongate and tilted steeply adaxially (Pl.8, fig.3), reflecting the configuration of the steep-sided calice. Presepiments are prominent, sometimes thickened, but in some corals can be very thin and outspread (Pl.9,

fig.2), apparently providing support for the coral on or in surrounding soft sediment. The dissepimentarium expands and contracts, with one to three or four rows of large dissepiments.

Type Specimens.—Holotype, UMMP 7838 (2 new thin sections, Pl.8, figs.1,2), paratypes FMNH 26004, 26005.

Discussion.—*Tabulophyllum rotundum* is morphologically very similar to *T. rectum*, but is differentiated by the nature of the lonsdaleoid dissepimentarium. Associated with this is a flaring of the corallite near the calice, which is largely the result of an increase in dissepimentarium size. The presepiments in some individuals form very large, thin sheets over adjacent sediment, and would have been effective in distributing the weight of the coral over a large area. If this feature is an adaptation to substrate, then *T. rotundum* may be an ecophenotype of *T. rectum*, adapted for life on fine, soft sediment. It is treated here as a separate species because its paleoecology is not well known.

Tabulophyllum rotundum Spassky (1960, p. 26) from the Middle Devonian of the Altai Region of the Russia is a junior homonym; the name of this taxon was changed by him to *T. manifestum* Spassky (1971, p. 106).

Tabulophyllum sylvaticum Rohart (1988, p. 244) very closely resembles *T. rotundum*, and should be synonymized with it. Especially the photographs of the holotype and paratype specimens (Rohart, 1988, pl. 29, figs 4,5) are very close to the paratype of *T. rotundum* illustrated here in figure 3 of Plate 8.

Occurrence.—In Iowa, *Tabulophyllum rotundum* only occurs in the upper Cerro Gordo. The holotype was collected from these beds at Bird Hill (Locality 31, Appendix); the two paratypes came from the Type Lime Creek (Locality 28). I collected specimens from Bird Hill and from Bird Hill North (Locality 30). The species is also known from the Frasnian Ferques Limestone of the Boulonnais region of France.

Tabulophyllum ellipticum

(Hall and Whitfield, 1873)

Plate 9, figures 4–9

Chonophyllum ellipticum Hall and Whitfield, 1873, p. 233, Pl. 9, fig. 13; Fenton and Fenton, 1924, p. 29, Pl. 3, figs. 5–8.

Diagnosis.—Medium-large elongate ovoid species of the genus, having a broad, short corallum with a wide elongate base, 90 to 94 septa, poorly developed minor septa commonly discontinuous or with wedge-shaped form adjacent to thick presepimental walls. Dissepimentarium narrow relative to tabularium, filled with abundant presepiments. Tabulae complete at several levels.

Description.—The two specimens available for study are the neotype (Pl.9, figs.4–7), and one slightly crushed specimen collected from upper Cerro Gordo beds (Pl.9, figs.8,9). The neotype is elliptical in outline, with a long axis of 34 mm and a minimum of 19 mm, while the other is 46 to 50 mm maximum and 25 to 26 mm minimum (with variation between two transverse sections). In transverse, both specimens show numerous dilated, spear-shaped major septa that are thick in the dissepimentarium and very thin in the tabularium. Septa are long and extend nearly to the axial plane of the coral. Septa are numerous, with a total of 94 septa in the neotype in which minor septa only reach to the innermost dissepimentarium, and 89 (that can be counted) in the other, partially recrystallized specimen. In the latter, minor septa are discontinuous (Pl.9, fig.8), but still have heavy, wedge-shaped bases on presepiments, and both major and minor septa have wedge-shaped bases on the outer wall of the coral. The transverse view is dominated by the heavy bases of septa against walls and presepiments with heavy stercome on the latter. Septa thus are somewhat dilated, uncommon for *Tabulophyllum* species in the Cerro Gordo.

In longitudinal view corals are short and broad with a very wide tabularium shown in the long axis view (Pl.9, fig.5), and with tabulae complete where not interrupted by axial ends of the septa, but commonly showing disruption. As typical for the genus, a peripheral trough is present at the margin of the tabularium. The dissepimentarium has dissepiments and presepiments of various sizes, and major change in diameter of the coral is accomplished by rapid changes, both in width of dissepiments and in size of elongate, inclined presepiments.

In longitudinal sections septal structure is very finely trabeculate, with trabeculae inclined adaxially, as is general in the genus (Pl.9, fig.6).

Type Specimen.—Neotype, USNM 78624 (specimen figured by Fenton and Fenton, 1924, Pl.3, figs. 7,8, noted as "C.L.W.", from the Webster collection.

Discussion.—The species was established by Hall and Whitfield in 1873, who noted it (*Chonophyllum ellipticum*) as "Coral small, subturbinate, laterally compressed, and much distorted in growth;". This description leads one to wonder whether they were including smaller forms in *Chonophyllum ellipticum* that are regarded here as *Tabulophyllum ehlersi*, along with the larger specimens included by Fenton and Fenton in the former (1924, p. 20). The Hall and Whitfield holotype has been lost. Of the two or three specimens figured by Fenton and Fenton (Plate 3, figures 5–8) only one has survived, that of figures 7 and 8, which was in the Webster collection and is now USNM

78624. I designate this specimen as neotype, as it is the only available specimen that was placed in this species by Fenton and Fenton. The lost Hall and Whitfield holotype was collected "in the marly beds at Rockford, Iowa" (1873, p. 233), which indicates the Cerro Gordo Member of the Lime Creek Formation. The Webster specimen (neotype) comes from Hackberry Grove, and also originated in the Cerro Gordo. The specimen collected by me at Locality 27, South Portland, is from high in the Cerro Gordo, in shales with abundant solitary corals occurring 4 to 5 m above the "rusty-weathering bed".

T. ellipticum is the only large species of the genus with an elongate oval outline, as seen here.

Occurrence.—The two specimens described here are from the upper part of the Cerro Gordo Member of the Lime Creek Formation. That noted by Hall and Whitfield likewise came from Cerro Gordo beds at Rockford. Except for the single specimen of *Tabulophyllum ponderosum*, these specimens of *T. ellipticum* are the largest solitary corals found in the Cerro Gordo beds.

Tabulophyllum ponderosum

Fenton and Fenton, 1924

Plate 10, figures 1,2

Tabulophyllum ponderosum Fenton and Fenton, 1924, p.40, Pl. 4, figs. 4,5, Pl. 5, figs. 5,6.

Diagnosis.—Very large solitary coral with wide dissepimentarium; both major and minor septa withdrawn from periphery. Major septa numerous, heavy, extend half way through tabularium. Dissepiments and presepiments numerous and varied, tabulae sparse and complete, flat to downbowed.

Description.—The single representative of the species is a very large corallite, 66 mm in maximum diameter; eroded on one side. The configuration of the eroded side marks this specimen as the paratype illustrated by Fenton and Fenton (their pl. 5, fig. 6); thus it is chosen as neotype. Its large size is very unusual among Cerro Gordo corals.

The species is unique, with its large size and wide, very well-developed outer dissepimentarium formed of varied presepiments interspersed with what seem to be normal dissepiments. Septa are numerous, with 60 major septa present in the one specimen, and presumably an equal number of minor septa, some of which have been eroded away. Fenton and Fenton recorded a range of 110 to 140 septa in the species, including the two lost specimens. Septa are restricted to the inner dissepimentarium and the tabularium. Major septa extend approximately $\frac{2}{3}$ of the way to the axis, and are dilated within the tabularium. The stereome coating

major septa in the tabularium also coats the innermost dissepiments to form a zone of heavily dilated skeleton in the inner $\frac{1}{2}$ of the coral. Some bilaterality is also present in this specimen, with major septa arranged pinnately around a shortened major septum, apparently the cardinal septum.

In longitudinal section, tabulae are flat, rather widely spaced and complete. At intervals these flat, complete tabulae are thickened by stereome (Pl.10, fig.2). There are well-developed peripheral gutters surrounding the tabularium in this specimen, as in other large species of the genus. The dissepimentarium is broad and contains numerous dissepiments. On one side of this specimen (concave side), the dissepimentarium is narrower and composed of sloping rows of uniformly sized, normal dissepiments with some larger elongate, flattened dissepiments (or presepiments) interspersed. On the opposite side of the corallite, the dissepimentarium is much broader, rows of dissepiments are more irregular and the sizes and shapes of dissepiments and presepiments are much more variable and somewhat more bulbous as well.

Type Specimen.—Of the holotype and two paratypes figured by Fenton and Fenton (pl. 4, figs. 4,5; pl. 5, figs. 5,6), only the paratype illustrated in their plate 5, figure 6 has been located (USNM 78623). The specimen is here chosen as neotype, as it is apparently the only specimen available for study.

Discussion.—*T. ponderosum* is as large as the largest species of the overlying Owen Member of the Lime Creek Formation, but is unique in the development of its extremely broad dissepimentarium and very large number of relatively small dissepiments within.

T. ponderosum of Iowa has characters in common with the late Frasnian species *T. zonatum*, reported from the Contadero Formation of New Mexico by Sorauf (1988, p. 160). *T. zonatum* is characterized by a short cardinal septum, dilation of septa in the two cardinal quadrants, an open area at the corallite axis, and numerous modestly sized dissepiments and presepiments, as is *T. ponderosum*. However, the very large size (66 mm diameter) and very large number of septa (total up to 140 major and minor) places *T. ponderosum* outside the range of variation seen in *T. zonatum*.

Tabulophyllum mcconnelli from Frasnian strata in northwestern Canada is also a large species of the genus. It is not as large as *T. ponderosum* (50 mm maximum diameter vs. 65 mm in the latter), does not have as many septa (approximately 100 total septa vs. 120 in the latter), and has less bilaterality than does *T. ponderosum*.

Occurrence.—The neotype is labeled as coming from Hackberry Grove, Iowa, which would indicate that it was collected within the Cerro Gordo Member

of the Lime Creek Formation. Fenton and Fenton stated that it occurs in the middle and upper part of the "Spirifer zone", which is the upper part of the member.

Tabulophyllum robustum Fenton and Fenton, 1924
Plate 10, figures 3–10

Tabulophyllum robustum Fenton and Fenton, 1924, p. 37, Pl. 5, figs. 1–3.

Tabulophyllum exiguum Fenton and Fenton, 1924, p. 37, Pl. 3, fig. 9.

Diagnosis.—Medium-sized corals with subturbinate to subcylindrical shape, large number of septa extending into tabularium. Corallite round, with generally narrow dissepimentarium and steeply inclined, elongate dissepiments. Tabularium broad with complete, flat-topped tabulae and peripheral gutters.

Description.—The five specimens placed with certainty into this species are medium sized, but large for the Cerro Gordo, with the holotype measuring 32 mm in diameter, the paratype 31 mm, and 22 mm for the holotype of *T. exiguum*, which is eroded and lacks part of the dissepimentarium. In each, the tabularium is from 11 to 18 mm in diameter in transverse section. Major septa vary from 39 to 48, with the total number of minor septa difficult to ascertain due to the state of preservation of these corals. Major septa are thin to dilated in the periphery, reaching several millimeters in thickness in the holotype (Pl. 10, fig.3), while remaining thin (less than 1 mm) in the other specimens. Septa are amplexoid, and may reach the axis of the corallite, but more often leave an open space in the axial region. Minor septa are thin and very discontinuous. In the holotype, minor septa are developed as short wedges at the outer wall (Pl.10, fig.3), but only as short spines on presepiments at the inner margin of the variably wide dissepimentarium (Pl.10, figs.5,7).

Longitudinal sections of *T. robustum* are characterized by a wide tabularium with complete and flat-topped tabulae, along with the peripheral gutter common in species of this genus (Pl.10, figs.4,6). The holotype exhibits a broad attachment base, but the base of the paratype is broken. Some specimens do not have a broad base of attachment, but instead a more pointed apical end. The dissepimentarium of the holotype is narrow and formed of steeply inclined rows of elongate dissepiments (Pl.10, fig.4). In the paratype, one side of the specimen has a greatly expanded dissepimentarium formed of large presepiments that are irregularly shaped as seen in transverse section (Pl.10, fig.6), and are greatly elongate and inclined. They may occupy the entire dissepimentarium. On this one side of the paratype, septa are pulled away from the outer wall, presumably as the coral expanded its exterior dis-

sepimentarium, apparently to avoid sinking into soft substrate.

Type Specimens.—Holotype USNM 78632A, paratype USNM 78632. *Tabulophyllum exiguum* holotype FMNH 26007.

Discussion.—*Tabulophyllum robustum* was established by Fenton and Fenton on the basis of two specimens in the Webster collection. I have also included *Tabulophyllum exiguum* in the species (Pl.10, figs.9,10). *T. exiguum* is a species based on a single specimen and no transverse section was made by the Fentons. They noted that it was characterized by an axial boss in the calice, but in transverse section, septa do not always reach to the axis of the corallite, as in other species of the genus with long septa. In this section, the holotype of *T. exiguum* strongly resembles *T. robustum*, where amplexoid septa do not generally reach the axis of the corallite. The two species are similar in size and number of septa. I thus regard *T. exiguum* as synonymous with *T. robustum*. Two additional specimens are also placed in the species.

Of the specimens of *T. mcconnelli* figured by Smith (1945, pls. 2,3), several would appear to conspecific with *T. robustum*. At present it is not possible to accurately determine exactly which are conspecific, and whether *T. mcconnelli* should be synonymized with *T. robustum*. This awaits restudy of the *T. mcconnelli* fauna from the Hay River area of western Canada.

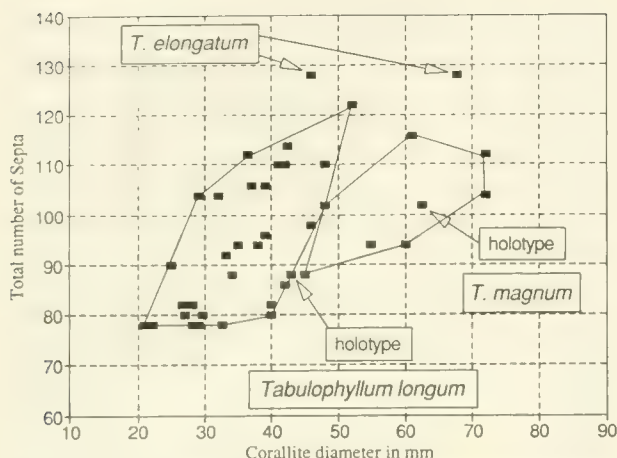
Occurrence.—The three museum specimens are labeled as collected from the "Spirifer zone" at Hackberry Grove, Iowa, thus the species occurs in the upper portion of the Cerro Gordo Member at the type section (Locality 28, Appendix). Two additional specimens collected by Calvin Levorson were from stripped material of the upper Cerro Gordo Member at the Rockford Brick and Tile Company Quarry (Locality 35).

Tabulophyllum longum Fenton and Fenton, 1924
Plate 11, figures 1–6; Plate 12, figures 1–5; Plate 13,
figure 1

Tabulophyllum longum Fenton and Fenton, 1924, p. 39, Pl. 3, fig. 1; Sorauf and Pedder, 1986, p. 1267, fig. 3; Sorauf, 1989, p. 401, Pl.4, figs. 1,2.

Diagnosis.—Species of the genus with 80–110 septa in adults and diameter up to 55 mm. Septa non-dilated, attenuate and long in adult corallites, with septa generally joined at axis, or with small axial open space. Tabularium broad with tabulae commonly flat and complete; dissepimentarium generally narrow with steeply inclined dissepiments and with lonsdaleoid dissepimentarium well-developed marginally.

Description.—*Tabulophyllum longum* is a medium large species, and the most abundant solitary coral of the Owen. In 27 post-juvenile (relatively mature) in-



Text-figure 31.—The large diameter corals from the Owen Member, *Tabulophyllum longum*, *Tabulophyllum magnum*, and *Tabulophyllum expansum*, with corallite diameter (in mm) plotted versus the total number of septa in each corallite. The holotypes of *T. longum* and *T. magnum* are identified. The holotype of *T. expansum* is the larger individual of the two plotted. The reason for overlapping in size between species is that immature specimens of *T. magnum* have a small enough diameter to fall within the field of *T. longum*.

dividuals, the range in corallite diameters is from 21 to 55 mm. The same corals have a range of from 39 to 52 major septa (Text-fig. 31). In the nine individuals in this sample that have 40 major septa or more, the mean diameter is 39 mm with a mean number of major septa of 54. These are representative of mature individuals in this species.

Tabulophyllum longum is a trochoid coral which may approach 70 mm in length, although this is not seen often, due to decortication of large specimens. In weathered-out specimens the calice displays a flat-bottomed calicinal pit approximately 20 mm in diameter and 13 mm deep, with development of a slight boss shown in a transverse section slightly below the calice, and with a narrow shelf surrounding the tabularial pit.

In transverse thin section the specimens commonly lack the epithecal wall (Pl.11, figs.1,3,4) present in unabraded individuals. Septa are numerous, and clearly differentiated into major and minor septa. Major septa are attenuate and extend to the axis of the corallite with only minor deflection at the axis. Septa are straight and long, with variable minor septa. These may be up to $\frac{3}{4}$ the length of major septa or much shorter, as little as $\frac{1}{5}$ the length of major septa. When well-developed they generally extend into the outer dissepimentarium. The cardinal septum is slightly shorter than other major septa and may be in a shallow fossula (Pl.12, figs.4,5). In the holotype, the cardinal septum is characterized by a lumpy, straight-sided dilation at the boundary between the tabularium and the dissepimentarium (Pl.11, fig.1), although this is not

characteristic of most individuals. In the tabularium, tabular segments appear as straight skeletal elements between equally straight septa. Dissepiments are straight to arcuate in the outer part of the corallite, and there are heavy rows of presepiments, forming inner walls. Presepiments do not disrupt major septa except right at the periphery of adult corals, although minor septa are interrupted around much of the periphery. The area of presepiments apparently was easily abraded and has been partly or mostly removed in many individuals. Large presepiments are not shown in the holotype except right at the periphery, although this is variable in large individuals. The species characteristically has a relatively narrow dissepimentarium.

Septal microstructure seen in transverse section is clearly of very fine monacanth trabeculae, which form a line of dark spots in the axial plane of septa, with flanks of fibro-normal calcite. Dissepiments, and in particular thickened presepiments, commonly have a lamellar to wavy-lamellar structure that is diagenetic in origin. A septotheca is seen in some individuals of this species.

In longitudinal section, *T. longum* shows features that would be generally expected in large species of *Tabulophyllum*; namely 1) tabulae interrupted in the axial area by long septa, while the outer tabularium is characterized (Pl.11, figs.2,5) by downbent tabulae forming "gutters", and 2) a dissepimentarium formed of several rows of relatively large, steeply inclined dissepiments, and which is narrow as compared to that of other large Iowa species of the genus (Pl.11, fig.5; Pl.12, fig.1). In *T. longum*, the dissepimentarium is generally composed of less than six or seven rows of dissepiments. It may be confused in transverse section with the outer tabularium, where incomplete tabulae are intersected by the plane of the section.

The tabularium is broad, varying in longitudinal section from 24 to 26 mm, filled with rather evenly spaced tabulae characteristically forming marginal troughs, with a smooth curve up to an elevated central area (Pl.11, fig.5). Amplexoid septa are interrupted at intervals, but only in the corallite axis. For the most part, septa interrupt tabulae throughout most of the tabularium.

The dissepimentarium comprises an arcuate series of vertically compressed ovate dissepiments with upwards of seven dissepiments per row, with each row steeply inclined (in excess of 75°) next to the tabularium, becoming progressively less inclined outward. The size of dissepiments varies, with larger dissepiments randomly distributed. No large presepiments are preserved in this section of the holotype or topotypes, in part at least, because the peripheral part of the corals has been removed by erosion. The dissepimentarium

is characteristically narrow, and is commonly lacking in juveniles. In each row, there may be as few as three to five steeply inclined dissepiments which tend to parallel the outer wall and thus cause the elongate coral shape.

Septal microstructure seen in longitudinal view is composed of very fine monacanth trabeculae arranged in an arcuate manner, perpendicular to the arch of dissepimental rows, and increasing axially in inclination (Pl.12, fig.3). The wall is a septotheca, formed by the expansion of peripheral portions of both major and minor septa.

In sections of juvenile corals, septa are dilated and invariably swirl around the corallite axis with no discernable cardinal-counter plane. Dissepimentaria are generally lacking and commonly only one row of presepiments appeared as the coral matured.

Type Specimens.—Holotype FMNH 26011, paratypes, USNM 78634 and 78634A.

Discussion.—This is the most abundant solitary species in the Owen Member. Numerous individuals have been collected from the southerly part of the study area, where the Owen was actively quarried. Young individuals with diameters of less than 1.5 cm are almost evenly divided between forms that have short, straight septa and others that have longer septa that swirl at the axis of the tabularium. These can lack a dissepimentarium or develop one which has two rows of dissepiments at most.

Development of the cardinal septum is somewhat variable. Many of the juvenile corals have recognizable bilaterality with a differentiated cardinal septum; these are forms with long septa. It is common in this species that the cardinal septum is short, with some bilaterality to the arrangement of septa, especially in the cardinal quadrants. Small individuals with short septa tend to lack bilaterality. Adults are most generally characterized by a short cardinal septum and/or a long counter septum and accompanying bilaterality. Figures 4 and 5 of Plate 12 illustrate in part, the variable nature of adults of this species in the length of their cardinal septum and development of symmetry.

In longitudinal section, where septa are amplexoid at the axis of the corallite, an arched irregular structure is present axially in *T. longum*. Seen in transverse sections of the holotype (Pl.11, fig.1), this structure is formed by arching of a tabula interrupting septa, which are then based on the tabula. Axially to this amplexoid base, septa have a very irregular path, and are variable in length and thickness. That the structure is irregularly developed in the species can be seen in some transverse sections, as well as the longitudinal section of the holotype. This forms an axial boss in the calicinal pit of the mature corallite.

Tabulophyllum longum is typical of large species of the genus, and thus resembles other large species; not only those found in the Owen Member of the Lime Creek, but in other Frasnian outcrop areas. It resembles in size the large species *Tabulophyllum zonatum* from Frasnian rocks of New Mexico, but differs from this species by the strong bilaterality and shorter septa of *T. zonatum*. It also can be compared to *Tabulophyllum smithi* Tsien, reported by Rohart from the Boulonnais region of France (1988, p. 242) and from the Ardennes of Belgium by Coen-Aubert (1982, p. 38), but the latter is characterized by large presepiments around the corallite periphery. These are not seen in *T. longum*. Some corals assigned to *Tabulophyllum mcconnelli* from the Hay River area of western Canada by Smith (1945, p. 59) may well belong in the Iowa species, but such a decision awaits restudy of the western Canadian fauna. Other large species of the genus are known, but their pronounced bilaterality makes them distinct from this Iowa species.

Occurrence.—Fenton and Fenton (1924, p. 39) stated that *T. longum* is found in the Owen, particularly in what they referred to as the “*Acervularia* zone”, the uppermost beds of the member. Individuals of *Tabulophyllum longum* occur in the uppermost beds of the Owen at the Lillibridge Quarry (Locality 38, Appendix), the Buseman Quarry, south of Dumont, Iowa (Locality 40), the North Buseman Quarry (Locality 40A) and, also from the uppermost beds of the member at the Carrolus Quarry (Locality 41, Appendix).

Tabulophyllum magnum Fenton and Fenton, 1924
Plate 13, figures 2–7; Plate 14, figures 1–5; Plate 15,
figure 1

Tabulophyllum magnum Fenton and Fenton, 1924, p. 38, Pl. 3, fig. 2, Pl. 4, figs. 1–3; Sorauf, 1989, p. 401, Pl. 2, figs. 2–5, Pl.3, fig. 3, Pl.4, fig. 4. not *Tabulophyllum magnum*, Tsien, 1976, p. 267, Pl. 2, fig. 3.

Diagnosis.—Large species of genus, with diameters up to 75 mm, and total of 100 to 128 long septa that join at the axis or swirl to form axial boss. Dissepimentarium wide with prominent marginal presepiments; dissepiments and septa dilated in inner dissepimentarium to form solid or semi-solid rings around tabularium. Tabulae generally incomplete.

Description.—Ten specimens assigned to *T. magnum* are large, ranging in diameter from 34 to 72 mm with a mean of 56 mm. Of these, seven more or less adult individuals range from 60 to 72 mm, with a mean diameter of 60 mm (Text-fig. 31). The number of major septa in these seven corals ranges from 47 to 58 with a mean of 54. The total range in number of major septa in the ten individuals is from 44 to 58, with a mean of 51.5.

The species is large, with an oval outline. The diameter of the tabularium is large, but generally is not more than $\frac{1}{3}$ to $\frac{1}{2}$ of the total diameter, with a large and prominent dissepimentarium occupying the rest of the corallite (Pl.13, figs.2,5). There are a large number of septa, equally divided into major and minor septa. The septa are long, and the cardinal and counter septa are commonly differentiated from the rest, especially the cardinal. Septa in the cardinal quadrant may also be arranged pinnately to the cardinal septum. Minor septa are well developed and commonly are more than $\frac{2}{3}$ the length of the long major septa. Septal dilation is prominent in the inner dissepimentarium.

In transverse section the dissepimentarium appears filled with numerous dissepiments similar to herringbone dissepiments (Hill, 1981, p.F24). Both septa and dissepiments are thickened in the inner dissepimentarium and outer tabularium (Pl.13, figs.2,3). Septal dilation also occurs here, and two to three rows of prominent, thick, steeply inclined dissepiments occur at this junction. Most septa join at the axis and there is a recognizable axial structure, although no raised boss is seen in the calicinal pit of the holotype.

The development of presepiments is not widespread, and generally only interrupts one major septum (Pl.13, fig.5). Presepiments are rare in the holotype, although this is perhaps at least partially due to corrosion and decortication during weathering; thus an outer, perhaps more lonsdaleoid dissepimentarium may be missing. No epitheca is visible. In other specimens of the species (Pl.14, fig.2), the occurrence of presepiments is more common in the outer dissepimentarium than in the holotype. Here too, presepiments seldom interrupt major septa although all septa are discontinuous near the periphery of the corallite.

In longitudinal section, the broad, arcuate dissepimentarium is prominent, with dissepiments of various sizes seen forming rows with numerous small flattened forms with interspersed larger, more bulbous dissepiments (Pl.13, figs.3,4,6). These rows reflect the shape of an arched calicinal platform. The innermost part of the dissepimentarium is marked by presence of abundant stereome. Here steeply inclined innermost dissepiments are thickened to form rows prominent in transverse section.

The tabularium is complicated by the presence of numerous long septa, so that virtually no complete tabulae are seen. Lateral gutters typical of the genus are developed (Pl.14, fig.1), and there is a flat-topped, arched aspect to the tabularium at the axis.

Septal structure seen in longitudinal section is composed of thin, monacanth trabeculae which arch over and in towards the tabularium (Pl.15, fig.1), and centrally are oriented parallel to the axis. Septa are rec-

ognizably amplexoid when seen in longitudinal view, with heavy trabecular bases developed across the tops of tabulae (Pl.14, fig.1).

Juvenile stages of the species are characterized by inflated septa that swirl around the corallite axis. At a slightly more advanced stage (Pl.13., fig.7), corallites tend to have long septa joined at the axis and display bilaterality due to the elongation of cardinal and/or counter septa across the axis and a somewhat pinnate arrangement of the septa.

Type Specimens.—Holotype FMNH 26009, paratype USNM 78633.

Discussion.—*T. magnum* has been identified from Belanski and Webster collections, all of which originated from a since disappeared collecting locality $\frac{1}{2}$ mile upstream from the Claybanks on the Winnebago River (Locality 28, Appendix).

Among the complex of small *Tabulophyllum* collected at the southerly localities (Localities 39, 40, 41, Appendix) are a number of individuals that could be young *T. magnum*, but only one was assigned with certainty to this species because of its elongate, pinnate bilateral nature which strongly resembles sections through youthful parts of large, mature *T. magnum* from farther north, near the Winnebago River.

The largest specimen of *Tabulophyllum magnum* seen in this study (Pl.14, figs.2,3) was collected from upper Owen beds at the Lillibridge Quarry (Locality 38, Appendix). The outline of the coral is rounded, with a diameter of 70 mm, and 56 major septa present. The major septa are long, and swirl around at the corallite axis so that there is no open space. The specimen was collected from rock matrix, rather than weathered out, thus the outer dissepimentarium is well preserved and adds much information regarding its morphology. Dissepiments are thickened by stereome in the innermost dissepimentarium, as common in this species, are very numerous and are uniformly arched away from the corallite axis (Pl.14, fig.3), sometimes sharply, sometimes smoothly arched. Where presepiments are developed, they are large and are elongate at the periphery. Both major and minor septa are interrupted by the well-developed presepiments in the outer dissepimentarium.

The longitudinal section of this large specimen shows the leaf-like expansion of both presepiments and dissepiments. It appears that many dissepiments formed on the presepiments that were covering sediment lateral to the main coral. The dissepiments are extremely low and flat at the periphery and these low, flattened forms are steeply dipping at the margin of the tabularium. Tabulae are generally complete, and are flat or sagging between septa in the axial region. Nine or more large open spaces are seen in the tabu-

larium in longitudinal section. It is not clear what the relationship is between these tabularial "gaps" and expanding and contracting of the corallite diameter, as shown by the leaf-like expansions of the dissepimentarium (Pl.14, fig.3). It is clear that the entire corallite was affected by environmental changes, most probably connected to rate of sedimentation.

Other large, bilateral species of the genus are known, and resemble *Tabulophyllum magnum*. One of these is *Tabulophyllum zonatum* from the late Frasnian Contadero Formation of south-central New Mexico. However, *T. magnum*, with its long septa, spear-like septal dilation in the tabularium, and lack of large presepiments in its periphery, does not resemble the New Mexico form other than superficially. The only other species that closely resembles *T. magnum* is *T. expansum*, which is undoubtedly very closely related, and possibly conspecific.

Occurrence.—Fenton and Fenton (1924, p. 38) noted that the occurrence of *T. magnum* is in the Owen Member, and "generally found in detritus". I found no specimens of the species in the northern outcrop area, but assume from the area where these were collected that they derived from the upper part of the Owen, the so-called "*Acervularia* zone" of Fenton (1919). In my collecting of Owen Member corals, most of *T. magnum* came from the uppermost beds of the member. The one largest individual was collected from the Lillibridge Quarry (Locality 38), and others at Buseman Quarry (Locality 40) and Carrolus Quarry (Locality 41).

***Tabulophyllum expansum* Fenton and Fenton, 1924**
Plate 15, figures 2–6

Tabulophyllum expansum Fenton and Fenton, 1924, p. 39, Pl. 2, figs. 11, 12.

Diagnosis.—Species defined originally on external form, which is short and broad. Species has very large diameter and long septa which swirl around axis to form columellar boss.

Description.—Two specimens are placed in this species, the holotype and one other, less mature individual (Text-fig. 31; Pl.15, figs.2–6). The holotype is weathered, with epitheca removed, as typical for material from this locality (west of Type Lime Creek). No signs are seen of talons or base, as in the *T. magnum* holotype. A calicinal pit is present, 2 to 3 mm deep with a very slightly raised axial boss. Septa are long, and swirl to form a very low, arching boss approximately 10–20 mm high. The calicinal platform is not flat, but upwardly rounded, with its maximum elevation $\frac{2}{3}$ of the way in towards the boundary of the calicinal pit. Weathering of this specimen may have exaggerated the

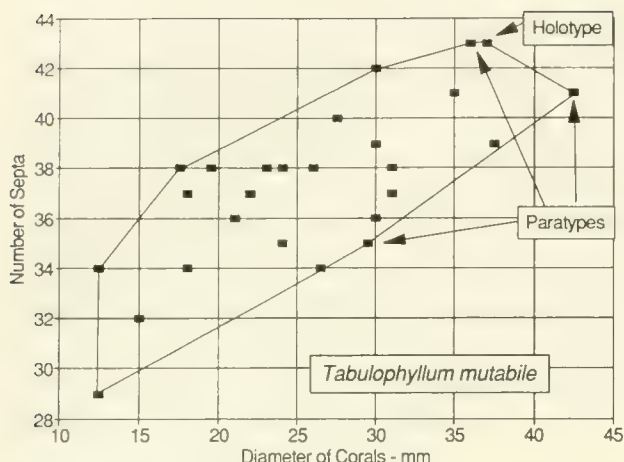
configuration of the upper surface. The species is oval in outline, with the outer diameter varying from 72 to 56 mm, and the oval tabularium having a maximum diameter of 43 and a minimum of 33 mm. Septa total 128 in the holotype, with clear differentiation into major and minor series. In transverse section, the axial area of the corallite is dominated by long septa that swirl counter-clockwise. Swirling septa are joined laterally by stereome to form a solid structure (Pl.15, figs.2,5). Septa are notably amplexoid, even at the axis, where a tabula forms a base beneath the swirled septal mass (Pl.15, fig.5). In the outer tabularium and innermost dissepimentarium septa are dilated, as in *T. magnum*. Together with one or two rows of heavy, dilated dissepiments, they form a heavy ring around the tabularium. The outer dissepimentarium is similar to that in *T. magnum* in that dissepiments are irregular, and presepiments occur rarely or not at all. This specimen was also decorticated during weathering.

In longitudinal section, the tabularium is flat but arches near the axis, with some complete tabulae and others that are low and vesicular. The amplexoid nature of septa is evident here (Pl.15, figs.3,4), more so than in *T. magnum*, although the shallow gutter seen in the periphery of the tabularium here is not as marked as in *T. magnum*. Dissepiments are varied in size with some large ones more typical in size and shape to those presepiments seen elsewhere in the genus. Dissepiments here form arcuate rows, steeply inclined at the innermost dissepimentarium and flaring outward to the periphery of the corallite. Most interior dissepiments are thickened where steeply inclined. Fine monacanth septal trabeculae are perpendicular to the rows of dissepiments, and thus incline progressively inward within the dissepimentarium, but are nearly parallel to the corallite axis in the tabularium, with a noticeable elbow at the boundary between the two areas.

Type Specimen.—Holotype, only specimen thus assigned by Fenton and Fenton, FMNH 26012. The only known topotype is SUI 3339.

Discussion.—This species is very closely related to *T. magnum*, and could be placed within the latter as a subspecies or ecovariant. It is characterized by a very large number of septa, in the neighborhood of 128 in total, while *T. magnum* generally has 20 fewer, even in mature individuals. *T. expansum* has a pronounced axial boss in addition to its extremely wide, flaring dissepimentarium. While the latter may reflect adaptation to soft substrate, the former is seen both in the adult holotype and in the other individual, a less mature form. With the present sample I prefer not to combine this species with *T. magnum*.

Occurrence.—*T. expansum* is very rare; the speci-



Text-figure 32.—*Tabulophyllum mutabile* n. sp. of the Mason City Member, corallite diameter (in mm) plotted versus the number of major septa within each individual. The holotype of this new species is indicated on the graph.

mens examined were collected long ago by Webster and Belanski, at a locality noted as 0.5 miles west of the claybanks on the Winnebago River. I was not able to find either an outcrop or specimens at this location, and assume that changes in topography or the course of the river during 75 years have obliterated the collecting locality.

***Tabulophyllum mutabile*, new species**

Plate 1, figure 6; Plate 16, figures 1–9; Plate 17, figures 1–4

Diagnosis.—Medium-sized species of the genus having well-developed presepiments in broad lonsdaleoid dissepimentarium, with no continuous septa therein. Axially, major septa are generally short and thin while minor septa occur as spines only on presepiments. Some individuals have identifiable cardinal plane and are weakly bilateral.

Description.—*Tabulophyllum mutabile* contains generally turbinate corals that flare outward as adults. Corallites are moderately large; for 24 individuals sampled, the total range in diameter is from 13 to 43 mm, but mature individuals vary from slightly less than 30 mm to 43 mm, and from 29 to 43 major septa (Text-fig. 32). Mature corals have a more narrow range, from 39 to 43 major septa.

Major septa may be long and reach to the corallite axis and swirl around it, or be long, with a small open space at the axis, or considerably shorter, with an open space of up to 5 mm at the axis (Pl. 16, figs. 1, 2, 6). The perceived length of septa partially depends on the position of the thin section in the corallite, because amplexoid septa are long where they have been sectioned in the axial region above a major tabula (Pl. 16,

figs. 3, 4), while appearing to be short beneath it. Major septa are thickest at the exterior wall, and are attenuate inward: they generally maintain a uniform width through the dissepimentarium and then thin into the tabularium. Minor septa are present only as spines, both on the exterior wall, and sometimes on presepiments in the outer dissepimentarium. The innermost presepiment has spine-like minor septa between each of the major septa (Pl. 16, figs. 2, 6). In the outer, lonsdaleoid part of the dissepimentarium, both major and minor septa are interrupted. On the external wall are spines of both that are equal in development and appear pyramidal in cross section.

In some corals, there is an identifiable cardinal septum, shorter than the others (Pl. 16, fig. 5; Pl. 17, fig. 1). Where this septum is short a weak bilaterality is developed and this also occurs in juvenile sections. Seen in transverse sections, the lonsdaleoid dissepimentarium is well developed in this species, presumably in response to rapid or abundant sedimentation. Individuals of *T. mutabile* may have up to five rows of very well developed presepiments which are large and irregular, and may be laterally elongate, up to $\frac{1}{3}$ of the total perimeter of the corallite (Pl. 16, fig. 6). Commonly both major and minor septa are only developed as spines on the presepiments, although major are stouter and longer. In addition, presepiments often have interstitial spaces filled with sediment which was perhaps included within the coral skeleton during rapid sedimentation. This may have triggered a resulting more rapid upward growth, with the ensuing formation of large presepiments by the polyps.

In longitudinal section, tabulae commonly are complete and subhorizontal, with wide spacing (as a result of rapid growth?), with both flat, regular tabulae forming bases for amplexoid septa and associated less complete irregular tabulae. It is common in this species that widely spaced tabulae have intertabular spaces infilled by sediment, just as presepiments are (Pl. 16, fig. 4; Pl. 17, figs. 3, 4). In some corallites this seems to occur at regular intervals, although more randomly in most.

Dissepiments seen in longitudinal section are abundant in some corallites, with their long axes inclined towards the corallite axis (Pl. 16, fig. 7). Presepiments tend to be very large, are peripheral to the dissepimentarium, and also are steeply inclined. In some corals, presepiments are rather bulbous in appearance in longitudinal section, but very elongate and generally infilled with sediment. The long axes of presepiments are generally parallel to walls of corals and flare when the walls flare.

The microstructure of septa is of very fine monacanth trabeculae in longitudinal section, with septal

bases expanded to form septotheca (Pl. 16, fig.9). Crystal fibers of septal bases are directed laterally to form the wall.

Sections of juvenile corals are characterized by short septa that are stout and tend to swirl somewhat around an open axial area. A lonsdaleoid dissepimentarium is seen, even in young specimens, but involves a single row of presepiments in these juvenile growth stages.

Type Specimens.—Holotype SUI 2247; paratypes SUI 1731, 141, 431, and 84745.

Discussion.—This is a highly variable species, but apparently one which was able to build skeleton rapidly, resulting in elongate corallites with wide lonsdaleoid dissepimentaria. Perhaps this was a response to rapid sedimentation. One of the striking aspects of the species is the wide spacing of tabulae and common infilling of intertabular spaces with sediment. This is also a species that was commonly bored by an unknown organism. Since no repair of holes was noted, the borings apparently were made after the skeleton was vacated by coral polyps. Boring is widespread in corallites of *T. mutabile*, but was not noted in any other species of Shell Rock corals.

Tabulophyllum mutabile cannot to be confused with any of the Lime Creek species. Small diameter Lime Creek species (such as *T. rectum*, *T. rotundum*) are all notably smaller than this abundant species of the Shell Rock Formation, while the larger species of the Lime Creek generally have characteristic septal dilation, bilaterality, and small presepiments, thus easily distinguished from the somewhat smaller *T. mutabile* with its very broad and large presepiments and general lack of septal dilation.

T. mutabile resembles the Frasnian species *T. ovinum* from the Sly Gap Formation of New Mexico (Sorauf, 1988, p. 163). The New Mexico species is about the same size as expressed by diameter, and number of septa as a medium-sized individual of the Iowa fauna. Both species have nearly radial septa and complete tabulae, but *T. mutabile* lacks the thick wall, broad septal bases, and obvious bilaterality of *T. ovinum*.

T. mutabile also has similarities with the species *T. longiseptatum*, reported by Soshkina (1951, p. 38) from Frasnian strata of Timan. The species are similar in size and number of septa and in having large presepiments. *T. longiseptatum* is characterized by the presence of complete, arched tabulae which serve to differentiate it from the Iowa form. *T. mcconnelli*, as described by Smith (1945, p. 59), very closely resembles some specimens of *T. mutabile*. Medium-sized individuals of the former are approximately the same size and contain approximately the same number of septa, which are undilated in both species. There is more bilaterality shown in *T. mcconnelli*, but the fact

remains that the two species are probably closely related, and the species from western Canada, when re-studied may be found to be the senior synonym of *T. mutabile*.

Occurrence.—*T. mutabile* occurs within the upper portion of the Mason City Member of the Shell Rock Formation, and has been collected from Localities 16 (Tom Williams Quarry), 17 (Baumgardner's Mill), 18 (Kapka's Farm), and 19 (Cooper's Bend, see Appendix). In addition, Belanski collected several specimens from the same level of the Mason City Member farther south, in the neighborhood of Greene, Iowa, on Coldwater Creek (Locality 126, Strimple and Leverson, 1969, p. 269).

Etymology.—The holotype and three paratypes are all selected from specimens collected by Belanski, whose collection labels bore this species name, apparently because the species shows considerable morphological variability.

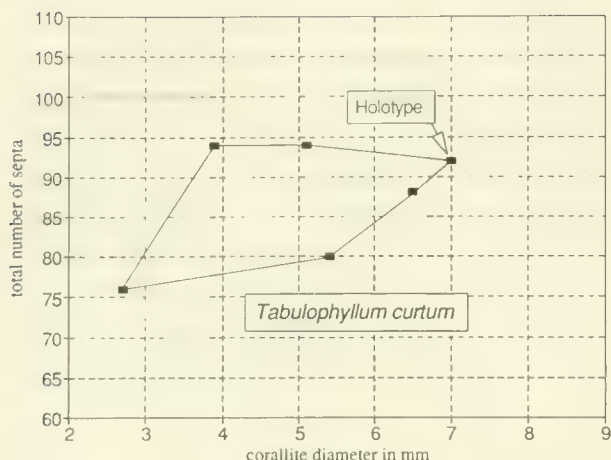
Tabulophyllum curtum, new species

Plate 1, figure 1; Plate 17, figures 5–11; Plate 18, figures 1–3

Diagnosis.—Large species of *Tabulophyllum* characterized by flaring turbinate form, large number of major septa and general development of lonsdaleoid dissepimentarium. Septa thick and minor septa more persistent than in most species of the genus. Corallites commonly deformed around or conforming to shape of neighbors.

Description.—These are large corals when mature, with a broadly flaring calicinal platform. For the six corals thin-sectioned, the mean diameter is 53 mm, with a range from 27 for an immature form, to more than 70 mm for the holotype (Text-fig.33; Pl.17, figs.5,6). The number of major septa ranges from 38 to 47, with a mean of 43.7. Mature corals of this species are normally in the neighborhood of 65 to 70 mm in diameter, with 46 or 47 major septa and an equal number of minor septa. Major septa are usually long and attenuate, leaving only a small open area at the axis. This characteristic is variable, and septa may attain the axis and leave only a small open area or none whatsoever. Major septa are heavy and maintain their thickness through the dissepimentarium into the tabularium. Minor septa are quite well developed, and are approximately $\frac{1}{3}$ the length of the major septa. This characteristic is very much dependent on the width of the lonsdaleoid dissepimentarium, and on deformation during growth of corals which were in contact with and grew around other organisms or hard objects.

Both the holotype (Pl.17, fig.5) and one paratype (Pl.17, fig.10) of *T. curtum* show a square-cornered indentation in the side of the dissepimentarium. In the



Text-figure 33.—*Tabulophyllum curtum* n. sp., from uppermost beds of the Mason City Member, corallite diameter (in mm) plotted versus the total number of septa in each individual. The holotype for this new species is indicated on the graph.

holotype, the corallite was laterally compressed where in contact with a foreign object, and has an expanded lonsdaleoid dissepimentarium on the side away from it. In the paratype, the presepiments of the lonsdaleoid dissepimentarium appear to have provided an enlarged surface, enabling the coral to spread over and around its neighbor. Where expansion of the corallite was not inhibited, a broad development of lonsdaleoid dissepimentarium resulted, with both major and minor septa discontinuous, either seen as spines on presepiments or as spinose bumps on septotheca. Where the corallite is laterally compressed (Pl.17, figs.5,9), septa are thick and complete, and minor septa are nearly as thick and $\frac{2}{3}$ as long as major septa.

Dissepiments seen in transverse view commonly arch peripherally or have an irregular form. Septa tend to be somewhat dart-like, thickening peripherally. The overall appearance of the dissepimentarium of these corals approaches the "herringbone" appearance (Pl.17, figs.5,8).

Longitudinal sections of these corals show a very broad and prominent tabularium, with tabulae commonly complete, sagging axially and upbowed towards the margin, with peripheral troughs commonly developed in large or flat individuals (Pl.17, figs.6,7). Dissepiments tend to be flattened, small, and only shallowly dipping towards the corallite axis. In one dissepiment, incremental centripetal growth can be seen in thin section (Pl.18, fig.3). Presepiments have the same orientation, and tend to be large, flat and elongate, and shallowly dipping, as they form the main skeletal elements for the flaring of the shallow cups.

The structure of the corallite wall is septothecal, with peripheral ends of septa dilated to form the wall

(Pl.18, fig.2), even though these septa may only be short spines in the outer lonsdaleoid dissepimentarium, when well-developed. The septal structure is composed of very fine monacanth trabeculae (Pl.18, fig.1).

Type Specimens.—Holotype PRI 44721; paratypes SUI 707, 1435 and 853, PRI 44722.

Discussion.—Although the types of this species show deformities by growth around neighboring objects, this is obviously a result of their microenvironment. Several specimens assigned to this species have an elongate ovate shape, and this apparently is the preferred form for individuals that have grown freely.

T. curtum, with its characteristic septal dilation and outer lonsdaleoid dissepimentarium, is dissimilar from most species of *Tabulophyllum*. This septal dilation is reminiscent of that seen in the large Lime Creek species, *T. magnum* and *T. expansum*, which however have their septal dilation more confined to the tabularium and innermost dissepimentarium, and have many more septa than the Shell Rock species. *T. densum*, described from Frasnian strata of Poland (Rozkowska, 1979, p. 42), has spear-like septal dilation of the same type as *T. curtum*, but differs by having a somewhat smaller size and heavier septal dilation.

Occurrence.—The sample available consists of three individuals collected by me from Locality 8, Nora Dam (see Appendix), while the other three specimens, from the Belanski collection, are from his former collecting locality approximately 200 meters north of the dam, the so-called Belanski's Quarry. At both localities specimens of *Tabulophyllum curtum* are found in the uppermost layer of the Mason City Member.

Etymology.—The species name for these corals is taken from cards in specimen boxes of the Belanski Collection. He had determined that this was a new species and had chosen this name. Apparently the term refers to the short, flattened form of the corals.

***Tabulophyllum levorsoni*, new species**

Plate 18, figures 4–7; Plate 19, figures 1–3

Diagnosis.—Large species of the genus, characterized by flaring shape, large number of septa and development of several stout walls formed by thick presepiments, resulting in inner lonsdaleoid dissepimentarium containing septa and an outer dissepimentarium lacking septa.

Description.—Five specimens varying in age and preservation range in diameter from 26 to 55 mm in diameter, with from 31 to 51 major septa. The means for this sample are 42 mm for mean diameter, and 43.5 major septa. Two of these specimens are immature, thus three mature corallites are 50 to 55 mm in diameter, with 49 to 51 major septa. Major septa are long

and extend well into the tabularium, but leave approximately $\frac{1}{2}$ of the tabularial diameter free of septa axially. Septa are straight and are attenuate in the tabularium. Minor septa extend only slightly into the tabularium. Septa are radially arranged, with only a slight hint of a pinnate arrangement around the cardinal area where there is a ladder-like appearance to dissepiments in transverse section (Pl.18, figs.4,7). Rows of dissepiments are curved outward when seen in transverse section, flattening peripherally. They are commonly thick and form concentric interior wall segments between septa (Pl.18, fig.4). Presepiments are large, always interrupt minor septa and sometimes also interrupt major septa. Septa are thick at presepiments and are dilated in the inner and medial parts of the dissepimentarium, then are attenuate in the tabularium. The outer part of the dissepimentarium is clearly delineated, as it contains presepiments only, without any septa except that both major and minor septa are part of the septotheca and occur as bumps on the outer wall. Both major and minor septa are complete in the inner part of the dissepimentarium but are present as spines only on presepiments.

The structure of the presepimental "walls" is most often lamellar, as common in *Tabulophyllum*, but from place to place a prismatic structure can be seen where the wall is less altered diagenetically (Pl.19, fig.1). The wall is septothecal (Pl.19, fig.2). Microstructure in septa in transverse section shows the axial plane of the septa formed of very fine monacanth trabeculae.

A longitudinal section of the same specimen reveals the tabularium characterized by many flat, complete tabulae, with incomplete tabulae sagging or leaning on them, and amplexoid septal bases shown (Pl.18, fig.5). In the periphery of the tabularium, gutters are developed uniformly on both sides, with upbowed tabulae arching before resting on the central tabularium formed of flat-topped tabulae. The dissepimentarium is formed of flattened elongate, steeply inclined dissepiments, which are irregular in size and shape and form rows which are inclined in a straight fashion, rather than arching upwards.

Septal structure shows fine monacanth trabeculae in longitudinal section, with trabeculae steeply inclined in the dissepimentarium, perpendicular to the rows of dissepiments. In the outer tabularium, growth lines can be seen as well as fine trabeculae (Pl.19, fig.3). The outer wall of the corallite is clearly septotheca (Pl.19, fig.2).

Type Specimens.—Holotype PRI 44723; paratypes PRI 44724, 44725, 44726, 44727.

Discussion.—*Tabulophyllum levorsoni* is unique due to a combination of its septal dilation, development of "inner" walls, and extensive presepiments. As

seen on Plate 18, figures 4 and 7, the presepiments occur in two bands, an outermost one at the extreme periphery of the dissepimentarium, with no through-going septa, and an inner one in which major septa are developed. Each of these bands is marked by a major thickening of presepiments to form a wall within the calice, with septa dilated to have a triangular base at the stereome of the inner walls. This characteristic, along with the ladder-like development of dissepiments in the cardinal area, separates the species from all other *Tabulophyllum*.

Occurrence.—All specimens of this species were collected from the basal portion of the upper biostrome of the Nora Member of the Shell Rock Formation at Locality 21 (Appendix), South of Rockford, Iowa.

Etymology.—The species is named for Calvin Levorson of Riceville, Iowa, enthusiastic student of Upper Devonian paleontology.

***Tabulophyllum buccinum*, new species**

Plate 19, figures 4–10

Diagnosis.—Medium sized species of *Tabulophyllum* with variable number of thick septa, well-developed lonsdaleoid dissepimentarium, and very thick wall.

Description.—Specimens assigned to this species have diameters ranging from 19 to 34 mm, with a mean of 27 mm. The number of major septa is variable, with a range of from 28 to 44, and mean of 34.5 for eight specimens sectioned. These numbers vary enough to suggest that the sample of eight does not properly characterize this population, restricted to a single horizon in the lower Nora biostrome.

Major septa are long to very long, either leaving a small open space at the axis, or withdrawn somewhat from the central tabularium. At various levels within corallites, septa are short, leaving the axial area open. Minor septa are variable, at most $\frac{2}{3}$ the length of major septa, and commonly only $\frac{1}{3}$ the length of major septa. The axial area is generally less than $\frac{1}{3}$ of the total area, without septa. Septa that are longer reach near the axial portion of the corallite. Septa generally taper inward from the septothecal wall.

In transverse section, the tabularium is characterized by the occasional appearance of tabulae, as seen in the plane of the transverse thin section. Intersection of septa with dissepiments commonly results in swelling of septa and deposits of calcite at the point of juncture. In transverse section, these corals show pronounced and well-marked lonsdaleoid dissepimentaria formed by large presepiments at the outer wall (Pl.19, fig.4). The presepiments are very large and few in number. The epithecal wall is generally a thick one, occasionally (Pl.19, figs.9,10) with a septothecal internal struc-

ture. These corals are commonly crushed as a result of compaction of reefy accumulations of skeletal material.

In longitudinal section, the species is characterized by flat-bottomed or sagging complete tabulae (Pl.19, figs.5,7). In the peripheral portion of the tabularium there is arching of tabulae. Dissepiments are small and steeply inclined adaxially. Corallites may have few or no dissepiments on one side and large, abundant, steeply inclined to sub-vertical dissepiments on the other side, probably reflecting reaction to change in orientation with respect to soft substrate. The external wall is prismatic in structure where very well-preserved, and has a septothecal structure (Pl.19, figs.9,10). Septa have small diameter monacanth trabeculae, with fibronormal structure both in septa and in epitheca (Pl.19, figs.9,10).

Type Specimens.—Holotype SUI 1282, paratypes SUI 1255, 1285, 141, and PRI 44728.

Discussion.—*Tabulophyllum buccinum* is a species of medium size and medium number of septa for the genus. Its very large dissepiments and presepiments apparently indicate that it should be treated as a separate species. These corals are difficult to categorize. Although not conspecific, *T. buccinum* resembles the Givetian species *T. traversensis* from Michigan.

Occurrence.—These corals are found within weathered outcrops of the lower Nora biostrome in the Reed Creek area, the "Reed Creek Phase" of Belanski (1927, p.359). The exception to this is one specimen, part of the Belanski Collection (SUI 1083), which is labeled as coming from the uppermost bed of the Rock Grove Member at Rockford (the "*Strobilocystites* zone" of Belanski, 1927, p. 353). Belanski noted that this bed is not present at any other outcrops of the Rock Grove Member, presumably being absent due to pre-Nora erosion (p. 353). Most solitary corals from the lower Nora apparently belong to *T. buccinum*, a poorly defined group which occurs in or adjacent to biostromal environments of the lower Nora.

Etymology.—The holotype and several other individuals assigned to this species were so named in collections by Belanski.

Tabulophyllum, species A

Plate 1, figure 2; Plate 20, figures 1,2

Diagnosis.—Medium-sized coral with smooth oval outline in transverse section, numerous long major septa, small open area at axis, and large bulbous presepiments forming lonsdaleoid dissepimentarium.

Description.—The only specimen of this species of *Tabulophyllum* has a smoothly rounded oval outline in transverse view. The diameter is 20 mm along the short axis and 32 mm on the long, with an open axial

area with diameters of 4 and 6 mm. The coral has 34 major septa, which are attenuate and numerous for this diameter. Major septa extend to the corallite axis with a small open area at the axis. Minor septa are present as spines on the outer wall, or may be more complete, and as much as $\frac{1}{2}$ as long as the major septa.

In transverse section the presepiments are large and bulbous (Pl.20, fig.1). The outer wall is septothecal, but has a weakly developed lamellar appearance in its outer portion.

In longitudinal section tabulae are steeply inclined in the outer part of the tabularium and flat-bottomed at the corallite axis where amplexoid septa are based on the tabulae (Pl.20, fig.2). The majority of tabulae tend to sag axially and have incomplete tabulae steeply stacked against the outer tabularium. There are abundant elongate, steeply dipping large presepiments and small dissepiments, all inclined axially at a large angle.

Discussion.—This specimen of *Tabulophyllum* appears to be a separate species, in which its oval form seems to be characteristic, along with its thick wall and large, bulbous presepiments and prominent internal walls.

Occurrence.—This coral was collected from the lower biostrome of the Nora Member of the Shell Rock Formation at Locality 4, Reed Creek (Appendix).

Tabulophyllum, species B

Plate 20, figures 3,4

Diagnosis.—Large ovate coral with elongate, thick septa. Minor septa well-developed and may approach thickness and length of major septa. Thick dissepiments and presepiments have an arcuate appearance in thin section.

Description.—This coral is large and oval in outline, with a long diameter of 50 mm and a short diameter in excess of 34 mm. There are 50 major septa, which are long and attenuate, reaching to the corallite axis or past it, thus no open axial space exists (Pl.20, fig.4). Septa are stout and thickest at presepiments, which interrupt both major and minor septa. Attenuate septa are thin in the tabularium, but thicken slightly near the axis. There are numerous thick dissepiments or presepiments and these generally bear minor septa as spines, even if only very short. In the outer wall, both major and minor septa are present only as bumps or short spines. Minor septa are well developed, especially at one end of the corallite, where they are uninterrupted and about $\frac{1}{2}$ as long as the long major septa. The septa join together at their bases and form septotheca on the outermost presepiment.

In longitudinal section the numerous large arcuate presepiments form much of the dissepimentarium

(Pl.20, fig.3). They are steeply dipping, with their long axes not varying much from the orientation of the wall. Tabulae are flat and straight in the axial area of the corallite and sag somewhat around the margins of the tabularium. Dissepiments are numerous with presepiments interspersed, but the two are so similar that it is not always possible to tell one from the other.

Discussion.—This single specimen, collected by Belanski, has septal dilation similar to that seen in *T. curtum* of the Mason City Member, and indeed could be conspecific. It is not placed in the latter due to its solitary occurrence in the collections made to date in Shell Rock beds, and its vertical separation from *T. curtum* of the Mason City.

Occurrence.—The coral is from the lower biostrome of the Nora Member of the Shell Rock Formation at a locality that he referred to as Baumgardner's Creek, but which has since been obliterated by quarrying operations at Locality 16, Tom Williams Quarry (Appendix).

Genus **TARPHYPHYLLUM**

McLean and Pedder, 1984

Tarphyphyllum McLean and Pedder, 1984, p. 27

Type Species.—*Tarphyphyllum besti* McLean and Pedder, 1984, p. 28.

Diagnosis.—Solitary or weakly fasciculate corals characterized by cylindrical form, fine septal trabeculae, weakly developed minor septa and lonsdaleoid dissepimentarium. Septotheca is thick.

Discussion.—The genus was established by McLean and Pedder to include, among others, four species from Frasnian strata in western Canada. These authors placed *Tarphyphyllum* in the Family Kyphophyllidae Wedekind, 1927, whose genera are united by the presence of very fine septal trabeculae, the development of presepiments and an accompanying lonsdaleoid dissepimentarium, and by characteristic complete tabulae in the very broad tabularium common in genera of the family.

McLean and Pedder (1984, p. 28) noted that *Tabulophyllum* can be distinguished from *Tarphyphyllum* by 1) being exclusively solitary, and 2) having a wider and better developed dissepimentarium. In the Shell Rock fauna, *Tarphyphyllum* apparently is closely related to thick-walled species of *Tabulophyllum*, and only separable from *Tabulophyllum* by the latter's characteristic development of lonsdaleoid dissepimentarium with multiple presepiments and a thin septotheca, whereas *Tarphyphyllum* generally has few or no presepiments and a very thick septotheca. The two genera, correctly placed together in a single subfamily of the Kyphophyllidae, are obviously very closely related, and might even be regarded as distinct only at

the subgenus level. The difference between the two in the Shell Rock biostrome of the lower Nora Member can be slight. A thick-walled species of *Tabulophyllum* at this level has septotheca much like that of *Tarphyphyllum*, while the latter, when a lonsdaleoid dissepimentarium is developed, is quite similar to the former. McLean and Pedder also remarked that *Tarphyphyllum* can be difficult to differentiate from some *Smithiphyllum* in Frasnian rocks of Western Canada. As all Shell Rock *Tarphyphyllum* are solitary or weakly colonial, there is no difficulty separating it from the fasciculate species, *Smithiphyllum belanskii*, the only other kyphophyllid seen in this unit.

Of the four species of *Tarphyphyllum* described by McLean and Pedder in 1984, only the type species, *T. besti*, is solitary. All of the Shell Rock specimens of this genus are solitary, with the exception of one individual which is twinned.

***Tarphyphyllum cylindricum*, new species**

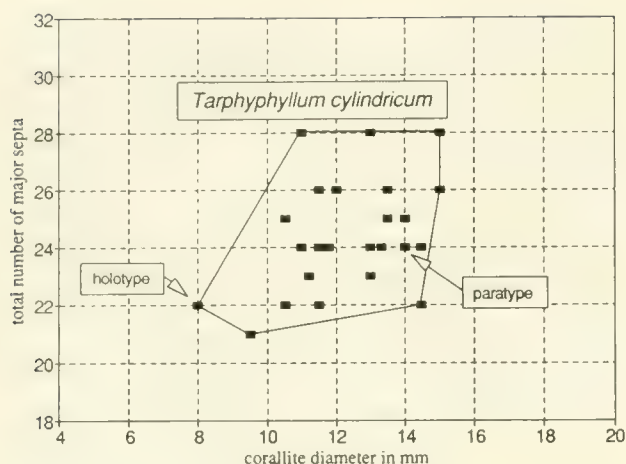
Plate 20, figures 5–10; Plate 21, figures 1–4,8

Diagnosis.—Solitary species of the genus with cylindrical growth form, sparse dissepiments, uniformly short minor septa, very thick septotheca and small diameter.

Description.—Individuals of *Tarphyphyllum cylindricum* are small, exclusively solitary and cylindrical in shape, with a moderate number of septa. The available sample consists of 24 corallites ranging in diameter from 8 to 15 mm, with a mean of 12 mm. The same corals have a mean number of major septa of 24.4, with a range of from 22 to 28 (Text-fig. 34).

Major septa are generally long, extending nearly to the corallite axis, leaving a small open area at the axis. In this sample, the open area ranged from nil to a maximum diameter of 4 mm, while the mean open diameter was 2 mm for 22 specimens. The major septa are amplexoid, and thickest at the corallite wall where they form septotheca, and they maintain their thickness throughout most of their length. If long, major septa may swirl somewhat around the corallite axis, but only a few of them are in lateral contact. Their perceived length is somewhat dependent on where thin sections are cut, because just below a dominant tabula, the open axial space is largest. Minor septa are always short, commonly no more than spines on the septotheca, but can be up to $\frac{1}{5}$ as long as major septa. Where a presepiment is well developed, minor septa occur as short spines on it. Major and minor septa together expand greatly at the wall to form the typical septotheca.

Where septa are short, tabulae are complete within the wide tabularium. Tabulae are rather irregular, with portions upbowed and wavy, especially over septal segments, and with peripheral gutters lacking (Pl.20,



Text-figure 34.—*Tarphyphyllum cylindricum* n. sp., from the lower biostrome of the Nora Member, corallite diameters (in mm) plotted versus number of major septa in each corallite. Holotype and one paratype for this new species are identified on the graph.

fig.5), or tabulae may slope axially from the margins of the tabularium and be sharply downbowed at the axis. Tabulae have a demonstrably fibronormal microstructure where sufficiently unaltered. Dissepiments and presepiments are rare and commonly engulfed by biogenic stereome of the wall or septa (Pl.21, fig.2). There are seldom more than two rows of steeply dipping dissepiments developed at any level within the corallites, and none whatsoever are present throughout most of the immature portions of the corallites (Pl.20, figs.5,8). The few dissepiments seen are elongate vertically, and have their long axis parallel to the cylindrical septotheca. Thus, a lonsdaleoid dissepimentarium may be totally lacking in the greatest part of most transverse sections of these corallites, which aids in distinguishing them from species of *Tabulophyllum*. The greatest development of lonsdaleoid dissepiments (rare) is up to $\frac{1}{4}$ to $\frac{1}{3}$ of the perimeter of the corallite.

Septothecal structure here is typical of *Tarphyphyllum*. Septal bases are composed of crystallite fibers directed laterally to join with those of neighboring septa to form a thick and complete wall (Pl.21, figs.1,8). In longitudinal section, these fibers are bundled in expanding crystallite clusters and are analogous to the septotheca seen in living scleractinians, except for mineralogy. In some specimens these laterally directed calcitic fibers have been modified into a pseudo-lamellar wall structure, especially on the outer rim of the wall.

Type Specimens.—Holotype SUI 1291, paratypes SUI 1290, 1250, and PRI 44730.

Discussion.—This species is not likely to be confused with described species of the genus. Although *T. besti* from western Canada may sometimes be sol-

itary, it is a larger coral, with diameters ranging from 13.5 to 16 mm, and with fewer septa, generally 24 or 25 major septa in mature forms. Minor septa are not seen except in the septotheca. The other Frasnian forms described by McLean and Pedder are all fasciculate.

Tarphyphyllum cylindricum is related to corals assigned to species of *Tabulophyllum* which occur in the same strata at the same localities. If this is an artifact of nomenclature, then it is a very convenient artifact. The construction of the septotheca in this species, and diagenetic modification of it in a few corals helps in understanding biocrystallization of the outer wall, as well as its diagenetic modification in species of *Tabulophyllum*, *Smithiphyllum*, and other kyphophyllids.

Occurrence.—All specimens assigned to *Tarphyphyllum cylindricum* were collected from the lower biostrome of the Nora Member. They occur abundantly in outcrops at Reed Creek, north of Nora Springs (Localities 3,4,5 Appendix) and sparsely in Locality 21 (Appendix).

Etymology.—The Belanski specimens were grouped in his collection and tentatively given this species name by him prior to his death.

***Tarphyphyllum*, species A**

Plate 21, figures 5–7, 9,10

Diagnosis.—Large diameter species of the genus characterized by oval form, numerous septa, and twinned form.

Description.—This large twinned cylindrical individual has an oval outline in transverse section, with diameters of 25 and 15 mm in one individual and 24 and 14 mm in the other, although the second corallite is eroded and its diameter altered (Pl.21, Fig.6). The former corallite has 34 major septa and the latter has 33.

The number of major septa in these two corallites is typical for species of this genus. Septa are amplexoid, and may be long, reaching almost to the corallite axis, so that one twin has a small open space (1.2 mm x 2 mm), while the other has much shorter septa in thin section, with a larger axial open space (5.3 mm x 9 mm). Length depends on where amplexoid septa are intersected by the transverse thin section. Major septa are thickest at the outer wall and progressively attenuated inward. Peripherally they expand to form the septotheca. Where major septa are long, they tend to swirl around the corallite axis, but leave a small open area at the axis. Minor septa are well developed but short. Where major septa are short, minor may be up to $\frac{1}{2}$ as long. Minor septa are broken by all prominent dissepiments and presepiments, and occur only as spines on septotheca and presepiments.

One individual has only minor development of a lonsdaleoid dissepimentarium at the two elongate ends of the corallite, while the other has presepiments extending laterally to form $\frac{7}{10}$ to $\frac{9}{10}$ of the perimeter (Pl.21, fig.6).

In a thin section of the juvenile part of the corallum, it is apparent that corallites are truly joined, and that the septa are amplexoid, with tabulae uparched, seen as ovals in transverse section (Pl.21, fig.5). One juvenile has 29 major septa with a minor diameter of 10.5 mm, and the other has 27 major septa where the minor diameter is 8 mm.

In longitudinal section, tabulae are dominantly steep sided and flat bottomed. Tabulae are clustered dramatically (Pl.21, fig.7). The clusters develop on a major, flat-bottomed tabula where amplexoid septa are based, and partial tabulae are developed as inclined or bowed or arched forms. The clusters are spaced 4 to 5 mm apart and each cluster has seven to ten tabulae per set. Presepiments and dissepiments are steeply inclined.

The structure of the septotheca is clearly shown in longitudinal section where spherulitic clusters of calcite crystallites make up the wall and peripheral parts of septa (Pl.21, fig.10). In transverse section of the adult part of the corallum, this septotheca is somewhat modified and beginning to take on a pseudo-lamellar aspect (Pl.21, fig.9).

Discussion.—This species is apparently unique among those assigned to *Tarphyphyllum* as it is of large diameter and has an oval cross section. The twin corallites are much larger in diameter than described species of the genus, including *T. besti*, the type species. Since I only have one specimen of this coral, I am not formalizing it, but simply report and figure it as a part of the Nora fauna.

Occurrence.—This single specimen originated in the upper biostrome of the Nora Member at locality 21, South of Rockford (see Appendix), and was collected by Calvin Levorson.

Genus **SMITHIPHYLLUM** Birenheide, 1962

Smithiphyllum Birenheide, 1962, p. 81; Pedder, 1965, p. 618; Hill, 1981, p. 229; Birenheide, 1986, p. 6; McLean and Pedder, 1987, p. 149.

Type Species.—*Spongophyllum imperfectum* Smith, 1945, p. 55.

Diagnosis.—(Following McLean and Pedder, 1987, p. 149) Fasciculate to subcerioid colonial coral with variably developed peripheral stereozone which does not interfere with development of dissepiments or presepiments. Presepiments generally large and steeply inclined, but may not be consistently developed throughout ontogenetic development. Major septa generally long and slender (but not in the Iowa fauna),

with minor septa variably developed. Tabulae are commonly complete and may be flat, or either arch or sag.

Discussion.—Birenheide (1962) erected the genus *Smithiphyllum* within the family Spongophyllidae to accommodate colonial species, mostly North American, with presepiments and thin sparse septa. These had been referred to the genus *Spongophyllum* by Stumm (1937, 1949) and Smith (1945). *S. imperfectum* (Smith) was selected as type species of the new genus. Pedder (1965) elaborated on the species of the genus, emphasized the relationship between *Smithiphyllum* and *Tabulophyllum*, placed both in the Endophyllidae, and authored the species *S. belanskii*, from the Shell Rock Formation of Iowa. The lamellar skeletal structure was described by Pedder from *Smithiphyllum* as being “that preserved” (avoiding the question of whether it is biogenic or diagenetic). I regard this as a secondary feature acquired during diagenesis of original skeletal structure (Sorauf, in press). Hill (1981, p. 229) followed Pedder in placing *Smithiphyllum* within the Endophyllidae.

Birenheide (1986, p. 6) also considered that a subgenus *Smithiphyllum* (*Smithiphyllum*) included all phacelloid species of the genus, while a subgenus *Smithiphyllum* (*Parasmithiphyllum*) McLean and Pedder, 1984, includes cerioid species. I prefer to leave these two distinct forms as separate genera, as proposed by McLean and Pedder.

McLean and Pedder's monograph (1987) on *Smithiphyllum* in western Canada, included all species known to date from North America, including *S. belanskii*, which occurs in western Canada as well as in the Shell Rock beds of Iowa. The reader is referred to this monograph for more extensive treatment of the genus and its species. The authors also discussed the Family Kyphophyllidae Wedekind, 1927, which includes among others, *Smithiphyllum*, *Tabulophyllum*, and *Tarphyphyllum*.

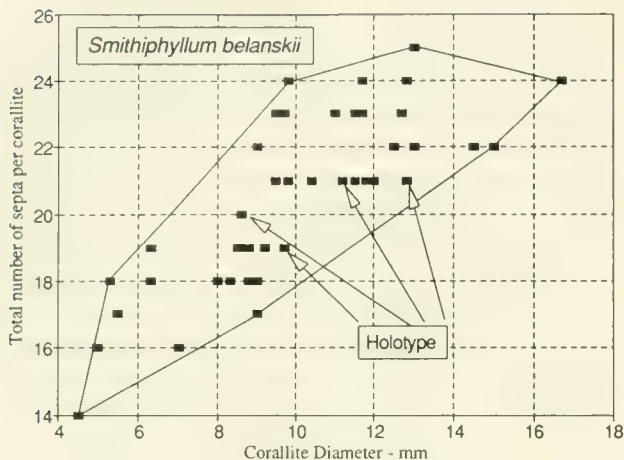
Smithiphyllum belanskii Pedder, 1965

Plate 22, figures 1–6; Plate 23, figures 1–5

Smithiphyllum belanskii Pedder, 1965, p. 623, Pl 88, figs. 1–3, 5, Pl. 89, figs. 13, 16; McLean and Pedder, 1987, p. 155, Pl. 5, figs. 1–5; McLean and Sorauf, 1989, p. 395, Pl. 3, figs. 5, 10.

Diagnosis.—Species of the genus with short, thin, somewhat radially arranged septa. Minor septa not noticeably developed. Young corallites commonly lack presepiments, but mature individuals have development of heavy interior wall surrounded by lonsdaleoid dissepimentarium with very large, steeply dipping presepiments. Septa present on exterior wall as low ridges only. Tabulae usually complete, flat where septa are present, but sag irregularly elsewhere.

Description.—*Smithiphyllum belanskii* is generally



Text-figure 35.—*Smithiphyllum belanskii*, from the lower, biospherical part of the Mason City Member, corallite diameter (in mm) plotted versus number of total septa for individual corallites of this colonial species. The four corallites described in the holotype colony are also indicated.

fasciculate, but where budding was frequent, it forms compact, subcerioid colonies. Walls in lateral contact become fused into a typical cerioid wall. Corallites are medium-sized, with diameters of mature individuals ranging from 8 mm to 17 mm, with a mean outside diameter of 11 mm in 37 corallites measured in eight colonies (Text-fig. 35).

In transverse thin section, corallites are marked by short, attenuate, spine-like septa with their greatest thickness at the wall (either the outer, epithecal wall or an inner wall formed by thickened presepiments). Septa all appear alike, and lack symmetry (Pl.22, figs.2,3,4,6). There apparently are no minor septa. The number of septa ranges from 14 to 25 in colonies studied, but mature corallites range from 18 to 25, with a mean number of 21.4 septa for 37 corallites in eight colonies (Text-fig. 35). Septa are generally not developed in the lonsdaleoid dissepimentarium where presepiments form open peripheral space. Septal ridges are sometimes developed on the inside of the epithecal wall and appear as stubs in transverse section. Septa are short in the tabularium; their length is generally $\frac{1}{3}$ to $\frac{1}{4}$ of the radius of the tabularium, so that there is always a large open space at the axis of corallites. At the extreme are corallites with only very short septal spines developed on the presepiments.

Presepiments are large, and single ones may occupy as much as $\frac{1}{4}$ of the perimeter of the corallite (Pl.22, figs.2,3,4). The inner wall formed by presepiments is commonly thick and may be angular as a result of interfering presepiments. Corallites may reach considerable size in some colonies prior to formation of presepiments, and have thick external walls. The largest

of these has an outer diameter of 8.8 mm and contains 19 septa. In a compact colony such as that seen in Plate 22, Figure 6, the heavy walls of corallites are compressed against those of neighbors, approaching a cerioid colonial form. Various stages of development are seen, with presepiments commonly not formed until attainment of considerable size. Some corallites commence formation of presepiments in corners rather early in their growth.

In longitudinal view, tabulae dominate the skeletal structure (Pl.22, fig.1). Tabulae are commonly complete and flat, especially in the space between septa, where septa are present. Where presepiments are formed, they are greatly elongate downward so that the calice had a very deep pit, with a flat floor composed of tabulae, and steep sides formed by presepiments. Presepiments tend to fill in bulges in the corallites where walls expand outward. Where septa do not extend into the tabularium, tabulae tend to be irregular and sagging. Tabulae in these colonies (Pl.22, fig.5) thus are much more irregular than typical, and they are characterized by regions of even greater irregularity, both in completeness and configuration of the tabulae.

The microstructure of septa and walls is extremely well-preserved in some Iowa specimens. Septal structure shows very fine monacanth trabeculae, with an approximate diameter of 0.1 mm (Pl. 23, fig. 2 shows about 27 in 3 mm). Seen in longitudinal sections they make a high angle with the corallite wall (inclined 70° inward). Where unaltered, the structure of the corallite wall is fibro-normal and septothecal (Pl.23, figs.3,4,5), not lamellar as frequently noted in the literature.

Type Specimens.—Holotype SUI 11616, paratype SUI 11617, both from the Mason City Member of the Shell Rock Formation at Nora Springs, Iowa.

Discussion.—The species was well described by Pedder (1965, p. 623), and additionally by McLean and Pedder (1987, p. 155). The latter noted that *S. belanskii* individuals from western Canada are larger than those from Iowa, ranging up to 2.0 cm in diameter, with up to 27 major septa (1987, p. 155).

Several specimens from the Mason City Member display remarkable preservation of epithecal wall structures (Pl.23, figs 1,3,4). These specimens are completely surrounded by encrustations of stromatoporoids, and this seems to help preserve the original structure from diagenetic change. Generally, the wall structure most often seen is modified lamellar, with septal bases affecting the development of (diagenetic) lamellar structure. This lamellar structure of walls is also very irregular in places. Diagenetic change was probably easiest in the fine crystals of the septa (Sorauf, in press).

Occurrence.—*Smithiphyllum belanskii* is found only in the basal biostromal unit of the Mason City Member. Pedder (1965, p. 623) reported that both the holotype and paratype were collected by him from the Mason City at Nora Springs. This is the type section of the Mason City (Locality 9, Appendix), where the basal biostrome is thick and well developed. Numerous topotypes were collected during the present study. The only other locality where *S. belanskii* was collected was from the Tom Williams Quarry, south of Nora Springs (Locality 16), where the lower biostromal unit is thin, but contains this coral species in its uppermost beds. These were the only localities where I was able to study the basal (biostromal) unit of the member.

Order **COLUMNARIINA** Soshkina, 1941

Family **CHARACTOPHYLLIDAE** Pedder, 1972

Pedder proposed the Charactophyllidae for solitary corals with coarse monacanth septal trabeculae that are “seen to be flexed first downwards, and then, provided the septa are sufficiently long, upwards, when traced adaxially” (1972, p. 698). This character unifies a group of genera that also show numerous globular dissepiments and variably dilated septa. I accept the definition of Pedder.

In the 1981 revision of the Rugosa for *the Treatise on Invertebrate Paleontology*, Hill placed the Charactophyllidae (with a query) into synonymy with her Subfamily Disphyllinae, in the Family Disphyllidae Hill, 1939 (1981, p. F264). She noted that, in the Disphyllinae, there are solitary, fasciculate and cerioid corals having septal trabeculae that are monacanths, and may be “parallel and steeply declined adaxially and waved at tabularial borders” (1981, p. F264). These were placed in a subfamily with genera having “half-fans” of trabeculae. This group of solitary genera with characteristic septal structure warrant treatment as a separate family, as proposed by Pedder.

Included in the family by Pedder are the Frasnian genera *Charactophyllum*, *Chostophyllum* and *Temnophyllum*. McLean (1993) has provided an overview of the family, including descriptions of the ten genera placed there by him. *Charactophyllum* is the only genus of the family represented in the Shell Rock and Lime Creek Formations of Iowa.

Genus **CHARACTOPHYLLUM** Simpson, 1900

Charactophyllum Simpson, 1900, p. 209; Fenton and Fenton, 1924, p.26; Smith, 1945, p.17; Stainbrook, 1946, p.415; Wang, 1950, p.219; Watkins, 1959, p.82; Altevoigt, 1963, p.14; Pickett, 1967, p.41; Pedder, 1972, p.698; Hill, 1981, p.F267; Pedder, 1982, p.562; McLean and Sorauf, 1989, p. 392; McLean, 1993, p. 109. not *Charactophyllum* Soshkina, 1949, p.90; Soshkina, 1951, p.68;

Spassky, 1960, p.50; Spassky, 1977, p.108; Birenheide, 1978, p.84.

Type Species.—*Campophyllum nanum* Hall and Whitfield, 1873, p. 232, Upper Devonian (Frasnian) Lime Creek Formation, Rockford, Iowa.

Diagnosis.—Solitary corals with charactophyllid septal structure of coarse monacanth trabeculae. Approximately 60 septa of variable length, with minor septa much shorter than the major septa, which may reach near coral axis and swirl in a counter-clockwise direction. Axial ends of septa commonly dilated and amplexoid. Dissepiments vary in number but always globular, arranged in steep rows, and vary in number from one to nine per row in the type species. Tabulae commonly complete and flat in axial portion of coral. Numerous steeply inclined tabular segments form transition zone between tabulae and dissepimentarium. In juvenile stages all septa long and dilated; in mature stages, septa alternately long and amplexoid, or short and withdrawn from corallite axis. Septa serrated (denticulate) along margin, but not carinate.

Discussion.—Interpretation of the genus *Charactophyllum* has been hampered by inadequate description and illustration of the type species, *Charactophyllum nanum* (Hall and Whitfield, 1873). The original species description by Hall and Whitfield, although vague and lacking an illustration of the type specimen, did note that the septa were “strongly denticulate on the edge” (1873, p. 232). Hall and Whitfield also recognized a species they named *Zaphrentis solida*, also characterized by denticulations on the septa, and with the same number of septa as *Campophyllum nanum*. This must be regarded as a synonym of *Charactophyllum nanum*, as discussed below.

When Simpson (1900) erected the genus *Charactophyllum*, he placed two species in it, the type species *Campophyllum nanum* Hall and Whitfield, 1873, and *Cyathophyllum radiculum* Rominger, 1876, a carinate form; this last, according to Rominger, originated in the Silurian of Drummond Island, Michigan, and Louisville, Kentucky (1876, p. 109). Stumm (1964, p. 51) later placed the Louisville specimens in the Silurian genus *Tryplasma*. The section of *Charactophyllum nanum* figured by Simpson (1900, p. 210, fig. 28) is a neotype (NYSM 3160/1) that was chosen by Simpson, since Hall and Whitfield did not specify or figure a specimen of *Campophyllum nanum*. It consists only of an overly thick, uncovered longitudinal “thin” section etched to make an acetate peel, which accompanies the specimen. Although lacking a transverse section, this longitudinal section shows the characteristics of the genus well, and is typical of the species in Iowa. Simpson’s written description of the genus, however, was

inaccurate in that *Charactophyllum* was described as carinate, "just as *Heliophyllum*" (1900, p. 210). Subsequently, some coral workers have continued to regard *C. nanum* as having carinate septa. It does not. The genus is not carinate.

Fenton and Fenton (1924) were the first, after Simpson, to study the Lime Creek corals, as part of their broader study of the strata and fauna. Although critical of the quality of Simpson's description of the genus *Charactophyllum*, theirs was also inadequate, dealing mostly with external characteristics and they also made the mistake of misusing the term "carinate", noting that, "the septa are strongly carinate, giving them a denticulate appearance in the calyx which does not, however, show well in the transverse sections" (1924, p. 25). On the same page they also noted that the carinate (read denticulate) septa are the diagnostic character of the genus. This is not an acceptable use of the term carinate, which must refer to structures expressed on the lateral flanks of septa, seen optimally in transverse thin sections.

An additional error of Fenton and Fenton was in placing the Hall and Whitfield species *Zaphrentis solida* into the genus *Heliophyllum*. This species is a synonym of *Charactophyllum nanum*; Fenton and Fenton noted that "septae are strongly denticulate" (1924, p. 28), and did not mention carinae such as those that typify *Heliophyllum*. No carinae are seen in the transverse thin sections of "*H. solidum*" and *C. nanum* illustrated by them, and the species are identical (1924, Pl. 1).

Smith (1945) and Stainbrook (1946) both illustrated topotypes of *Charactophyllum* from Rockford, Iowa, and their studies should have dispelled the notion that the genus has carinate septa. Although Smith wrote in his generic diagnosis that the genus has carinate septa (1945, p. 17), he figured transverse sections of three specimens that clearly show septa that are non-carinate. Stainbrook (1946, p. 415) noted that although the septal flanks appear to be "carinated", they are not "typical carinae similar to those of *Heliophyllum*", and "do not project into the interseptal loculi and are not evident in transverse and longitudinal sections". He preferred referring to the septa as "trabeculate rather than carinate" (1946, p. 415). This could have sufficed to indicate clearly the true nature of septa in this species.

Some workers however, have continued to believe that *Charactophyllum* is a genus of solitary corals with carinate septa. Soshkina (1949, 1951) placed carinate species within the genus, and in addition, included the presence of fan-like septal trabeculae in her diagnosis of the genus (1951, p. 68). She also noted (1951, p. 73) that *Heliophyllum* differs from *Charactophyllum*

only in that it has longer major septa which reach the corallite axis. Spassky (1960) accepted Soshkina's concept of the genus. Birenheide (1978, p. 84) noted that *Charactophyllum* has "clearly to strongly developed yardarm carinae on the septa". This is incorrect, and species placed in *Charactophyllum* by these authors must be re-examined.

Wang (1950), Watkins (1959) and Altevogt (1963) each studied and discussed topotypic material of the type species. Wang (1950, p. 219) observed the important characteristic, the "elbow-bending" of the monacanth septal trabeculae, later utilized by Pedder (1972, p. 698) as an important character of the *Charactophyllidae*. Watkins (1959) and Altevogt (1963) helped to define the genus by illustrating additional specimens from the Lime Creek Formation of Iowa.

Pedder, in two important papers (1972, 1982) has accurately diagnosed the genus, as well as providing an accurate and complete description of the type species (1982, p. 563). The papers of Pedder, along with the description by Hill (1981) insure that the genus *Charactophyllum* is now based on the morphology of *C. nanum*.

Range.—This genus is abundantly represented in Frasnian faunas of Iowa and also in western Canada (Pedder, 1972, p. 698) as well as in Spain (Altevogt, 1963, p. 15). The genus has also been reported from the Ural Mountains of Russia by Soshkina and by Spassky, and from the Eifel Region of Germany by Birenheide, but these reports are potentially erroneous, as noted above.

Charactophyllum nanum

(Hall and Whitfield, 1873)

Plate 2, figures 1–4; Plate 24, figures 1–15; Plate 25, figures 1–12; Plate 26, figures 1,2

Campophyllum nanum Hall and Whitfield, 1873, p. 232.

Zaphrentis solida Hall and Whitfield, 1873, p. 231, Pl. 9, fig. 5.

Charactophyllum nanum Simpson, 1900, p. 209, fig. 28; Fenton and Fenton, 1924, p. 26, Pl. 1, figs. 1–3; Smith, 1945, p. 17, Pl. 1, figs. 6, 7, 8a, 8b, Pl. 31, figs. 1a–1i; Wang, 1950, p. 219, Pl. 7, figs. 44a, 44b; Watkins, 1959, p. 82, Pl. 16, figs. 13–20; Altevogt, 1963, p. 15, Pl. 1, fig. 1; Hill, 1981, p. F267, figs. 171, 1a–f; Pedder, 1982, p. 562; McLean and Sorauf, 1989, p. 392, Pl. 3, figs. 8, 9.

Heliophyllum solidum Fenton and Fenton, 1924, p. 28, Pl. 1, figs. 4–7.

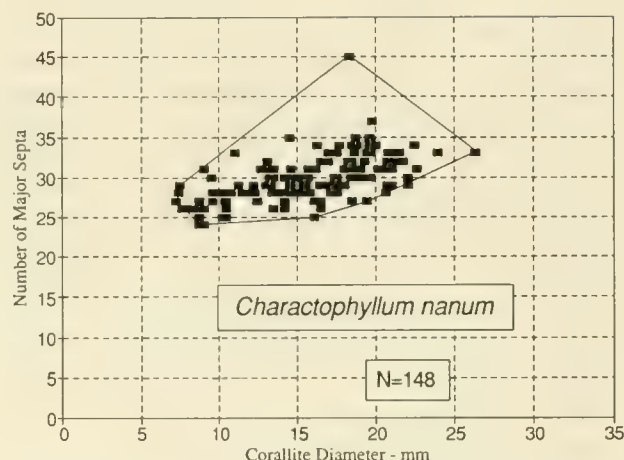
Diagnosis.—Type species of genus characterized by septa which are weakly bilateral in some individuals, with minor septa generally less than one-half as long as major; with distinctive septal structure, length variations and dilation. Non-carinate septa with coarse monacanth trabeculae which flex downward in the dissepimentarium, and then flex sharply upward in the tabularium. Septa partially amplexoid, with length

varying in major septa from long, reaching almost to the corallite axis, to short, leaving as much as one-third of the coral as open axial area. Dilation varies from heavy in periaxial area in long septa to light or absent in short septa. Dissepiments small, globose, in one to nine steeply inclined rows; tabulae commonly complete and flat, with numerous steeply inclined small tabulae forming transition to dissepimentarium.

Description.—*Charactophyllum nanum* includes corals of medium to small size with varying shapes, from trochoid to ceratoid (Pl.2, figs.1–4), with elongate forms more abundant. The calice is deep, flat-bottomed and steep-sided, reflecting steep rows of dissepiments. Septa in the calice are denticulate (having a toothed oral margin), and sides of septa are marked in the calice by subhorizontal ridges marking the positions of coarse subhorizontal monacanth trabeculae. These are later obscured by biogenic calcite in dilated septa. Thus, septa are denticulate, ridged and may be somewhat knobby in cross section, but definitely are not carinate.

In transverse section, septa of two orders are seen, with minor septa generally up to one-half the length of major septa. In 35 specimens with diameters ranging from 13 to 22 mm (mean of 15.4 mm) the number of septa range from 54 to 74 with a mean of 61.5 septa (Text-fig. 36). Seen in transverse section, septa appear knobby in the dissepimentarium, thickened at trabeculae and commonly also at the junction of dissepiments and septa. In adult parts of the corals, major septa commonly extend through $\frac{2}{3}$ to $\frac{3}{4}$ of the tabularium, leaving a small open area at the axis (Pl.24, figs.2,3,9,12,13). Septa may be weakly bilateral, arranged around a short cardinal septum (Pl.24, fig.3), or more typically, radially arranged with long septa swirled around the axial open space (Pl.24, fig.6); or septa may be short and radial, with a large axial open area (Pl.25, figs.1,5). The length of septa varies greatly during the life history of an individual. Septa are partially amplexoid, with maximum septal length occurring directly on and above a prominent thickened tabula. Septa in adult parts of the coral are usually dilated in the tabularium if they are long, with swollen, inflated septa deflected around the axial region (Pl.24, figs.2,3). Short septa have their maximum dilation near the outer margin of the tabularium (Pl.25, fig.5). Dilation of long septa forms an axial boss in some individuals. Dissepiments appear in transverse section as numerous arcuate intersections (with the small globose dissepiments). Where septa are dilated, dissepiments are commonly thickened by stereome. Where septa are long but less dilated, the innermost dissepiments are thickened and outline the tabularium.

In juvenile parts of *Charactophyllum nanum*, septa



Text-figure 36.—*Charactophyllum nanum*, the most abundant coral in the Cerro Gordo Member, corallite diameter (in mm) plotted versus number of major septa for individuals of this solitary species. Included are forms that fit the description of *Zaphrentis solida* Hall and Whitfield, here placed into synonymy. The single specimen with the large number of septa shown at the top of the graph appears anomalous, but resembles the other members of the species in all other ways than number of septa.

are generally thick throughout, and commonly are dilated to touch laterally (Pl.24, figs.5,8,15). Septa are long; normally the cardinal septum is short while the counter septum extends along through the axial area of the coral. Where only one or two rows of dissepiments occur in juveniles, they appear as a row of clear vesicles outside a zone largely filled with stereome.

In longitudinal section, several characteristics of the species (and genus) are clearly visible. The septa contain coarse, monacanth trabeculae (Pl.25, figs.8,12), which have the characteristic charactophyllid configuration (Pedder, 1972, p. 698). Seen in longitudinal section, trabeculae arise at an angle with the corallite wall and quickly bend to subhorizontal or more commonly, slightly past horizontal, in the dissepimentarium, then bend sharply upward at the outer boundary of the tabularium and continue upwards in the axial region of the coral.

The existence of prominent tabulae with heavily dilated septa on and just above it also seems characteristic of the species. Septa are amplexoid, with a heavy base and with their greatest length on a prominent, thick tabulae. There is an alternation of a corallite form with shorter septa below these tabulae, and a form with longer, more heavily dilated septa just above.

The dissepimentarium varies in longitudinal section, especially in the number of rows of globose, evenly-sized dissepiments. In adult parts of the corallite, there are from one to nine rows of dissepiments; generally there are more than three or four. Where there is a constriction in the coral diameter, there is a corre-

sponding decrease in the number of rows of dissepiments. More elongate ceratoid corals tend to have fewer rows than do trochoid corals. In curved forms, there are generally more rows of dissepiments on the convex side of the coral (Pl.24, fig.10).

Tabulae are generally somewhat flat and complete in the axial area (Pl.24, figs.4,10; Pl.25, figs.10–12). Periaxially, tabulae vary, but are commonly arched adorally, then are downbent to form a peripheral trough around the tabularium, or else are more irregular and incomplete marginally. Small lateral tabulae are abundant, forming a transition into the steep rows of dissepiments. These tabulae are elongate and adaxially inclined, with the same orientation as the rows of dissepiments. They may also be coated with stereome where they merge with prominent, thick tabulae. Spacing of tabulae varies periodically, with the greatest spacing just below thick, prominent tabulae with amplexoid septa above.

Type Specimen.—Simpson's neotype, NYSM 3160/1 is a very thick longitudinal section (1900, p. 209, fig. 28, p. 210).

Discussion.—Hall and Whitfield, although not figuring their species *Campothyllum nanum* (1873, p. 232) did describe and figure the species *Zaphrentis solida* (1873, p. 231). The descriptions of the two proposed species are similar, in that they both have a deep calice, denticulate septa, and a dissepimentarium with "minute" dissepiments. The difference, as noted by them, is that *Z. solida* is "turbinate" (p. 231) while *C. nanum* is "elongate-turbinate" (p.232). Both of these forms are common within the population of *C. nanum* studied by me. The type specimen of *Zaphrentis solida* is not present in the New York State Museum, and must be presumed lost.

Fenton and Fenton recognized two abundant species of solitary corals in the Cerro Gordo Member, *Charactophyllum nanum* (1924, p. 26) and *Heliophyllum solidum* (1924, p. 28). They noted that the more elongate form, *C. nanum*, is "the commonest rugose coral of the Hackberry" (p. 26), but also said that the "subconical to subturbinate" coral, *H. solidum*, "rivals *Charactophyllum nanum* in abundance" (p. 28). This is true, as sections of the Fentons' topotypes of *H. solidum* (FMNH 26002, 26003) are certainly conspecific with *C. nanum*. The latter is extremely abundant in the Cerro Gordo beds of the Lime Creek Formation, outnumbering all others.

In addition to variation in external shape, *C. nanum* also varies considerably in septal length and ornamentation, and in configuration of dissepiments and tabulae. Adult *C. nanum* vary a great deal in both length and thickness of septa. Two extremes are 1) corals with undilated septa, and either a large open axial area

with short septa (Pl.25, fig.5), or a small open axial area with elongate attenuate septa (Pl.25, fig.9); and 2) corals with long, dilated septa, with heavy dilation in the tabularium sometimes resulting in an axial boss (Pl.24, fig.2; Pl. 26, fig.2). Much less variation is seen in juvenile portions of the corals, where septa are invariably long, most often with a short cardinal septum and a long counter septum which extends across the axis of the coral. This bilaterality is variably preserved into the adult state. Some *C. nanum* adults show bilaterality around a short cardinal septum, but many more do not. Juvenile portions of *C. nanum* usually have dilated septa, and may be heavily filled with stereome, but some have much less heavy apical skeletons.

The shorter, trochoid corallites (the *Z. solida* form) most often have rather attenuate septa, especially so adjacent to the calice. In the calicinal area, the coarse monacanth septal trabeculae are shown in relief on the flanks of thin septa. This presence of almost horizontal trabecular ridges on the flanks of septa, accompanied by denticulations where the monacanth intersect the upper margin of the septa, impressed early workers and led to the false belief that these are carinate septa. Stainbrook later noted that "the ridges on the sides are due to trabeculae. The septa may be said to be trabeculate rather than carinate" (1946, p. 415). Where septa are dilated, these ridges are smoothed over by stereome in the thicker septa. The presence of these subhorizontal ridges is seen in longitudinal sections of septa where monacanth bend to the subhorizontal position in the dissepimentarium, and then bend sharply upward in the tabularium (Pl.25, figs.10–12; Pl.26, fig.1). This is the "elbow folding" of Wang (1950, p. 242), and the "characterophyllid trabeculae" of Pedder (1972, p. 698).

Variation in septal length and dilation is clearly seen within individual corals. In longitudinal section the amplexoid nature of these septa is seen in the periodic occurrence of sclerenchyme and septal trabeculae on some tabulae (Pl.24, fig.4). Transverse sections just above such a tabula show long, heavily dilated septa, where transverse sections just below have shorter and thinner septa which are not dilated in the tabularium. A series of sections in a single coral may show alternations of forms of the dilated *C. nanum* type (Pl. 25, figs.4,5,6) and forms closer to that regarded as *Z. solida* by Hall and Whitfield (1873) and by Fenton and Fenton (1924).

In longitudinal section, variation in the number, size and thickness of plates is seen in dissepiments and neighboring tabulae (Pl. 25, figs.10–12). The number of rows of dissepiments is highest in flatter (trochoid) corals, and may be very numerous, especially on the

convex side of the coral. The dissepimentarium may also expand and contract during the life history of the individual, possibly as a response to changes in sedimentation rate. Also, these corals may have lived with their skeleton at least partially buried in soft sediment, so that the dissepimentarium was both adjacent to sediments and adjusted to their presence.

There is also a variation in thickness and weight of tabulae and dissepiments, which apparently corresponds to periodic thickening of skeletal elements and building of long, dilated septa over them. This species is an extremely abundant one in the Cerro Gordo Member, and at the same time a variable one, with variation within individuals sufficient to encompass the variation which is seen in corallites where they form more elongate or less elongate shapes.

Two papers by Pedder (1972, 1982) have clarified both the genus and species of *Charactophyllum nanum* as well as relationships to other genera of Pedder's family Charactophyllidae. Descriptions of this species, as well as *Zaphrentis solida* show a history of misunderstanding of septal morphology because of misuse of the term "carination", and misapplication of the words "carinae" and "carinate" to the septa in these named groups. This history need not be further discussed here, except to note that *Z. solida* is best left lapsed. The use of *Campophyllum nanum* by Simpson and all other authors as the type species of *Charactophyllum* mandates allowing this. In the Cerro Gordo fauna, there are no other corals which could be confused with *Charactophyllum nanum* and there is no doubt as to the identity of what was called *Z. solida*.

Altevogt (1963, p. 15, Pl. 1, fig.1) additionally reported the species from late Frasnian rocks in Northern Spain. His illustrated specimen appears properly assigned to *C. nanum*, greatly expanding the geographic range of the species. Smith (1945, Pl.1, fig.6) also figured a transverse section through what he called *Charactophyllum* sp., and this appears also to be a specimen of *C. nanum*, although with question.

Occurrence.—*Charactophyllum nanum* occurs profusely in the Cerro Gordo Member at all outcrop localities. It was most abundant in the upper $\frac{1}{3}$ of the member at Bird Hill (Locality 31, Appendix) and adjacent outcrops. One specimen of *Charactophyllum* sp. cf. *C. nanum* has been found in the Owen Member at the Buseman Quarry, south of Dumont, Iowa (Locality 40). Also, the species apparently occurs in Frasnian strata of western Canada and Spain.

Family DISPHYLLIDAE Hill, 1939

In the 1981 revision of the Subclass Rugosa for the *Treatise on Invertebrate Paleontology*, Hill placed in the Disphyllidae solitary and colonial corals with mon-

acanth septal trabeculae which are, "commonly in half fans, or in fans" (1981, p. F264). This terminology is misleading, because these fans are not similar to, nor are these genera related to, corals with symmetrically branched septal trabeculae that form fans as genera in the Phillipsastreidae. In the Disphyllidae, some corals with wide dissepimentaria have gently arched rows of dissepiments, and a resultant arching of septal trabeculae perpendicular to them can form a weak "fanning" of trabeculae as seen in longitudinal section (illustrated by Strusz, 1965, p. 524). I prefer not to utilize the same term (fan) for two very different features characteristic of the two families.

While accepting in great part the generic composition of the Family Disphyllidae as defined by Hill, I modify her usage in the following ways:

1. I do not accept her subfamily Subfamily Hexagonariinae, which she considered should include cerioid disphyllids with closely carinate, long, fusiform septa (1981, p. F274). This is based on a misinterpretation of *Hexagonaria hexagona*, in which "carinae" can occur, but only as part of a process of septal dilation that includes the lateral expansion of trabeculae as part of the process, as discussed below under the genus. In this subfamily, Hill placed the genus *Hexagonaria*, which is closely related to *Disphyllum*, with *Haplothecia* and *Marisastrum*, which are not. I do not include them in this family, as discussed in Sorauf (1994, p. 333), and:

2. I exclude solitary genera with characteristic sharp flexing of coarse septal trabeculae, placing *Charactophyllum* and related genera into the Charactophyllidae Pedder, 1972, as noted above.

Genus DISPHYLLUM deFromentel, 1861

Cyathophyllum Goldfuss, 1826, p. 60 (in part).

Disphyllum deFromentel, 1861, p. 302; Stumm, 1949, p. 33; Pickett, 1967, p. 22; Rozkowska, 1960, p. 7; Tsien, 1970, p. 162; Rozkowska and Fedorowski, 1972, p. 296; Hill, 1981, p. F264; Rohart, 1988, p. 252; Sorauf, 1987b, p. 681; McLean and Sorauf, 1989, p. 392; Birenheide, 1978, p. 90 (in part); Birenheide and Gabrielli, 1993, p. 14 (in part).

Heliophyllum Fenton and Fenton, 1924, p. 27.

Diphyphyllum Fenton and Fenton, 1924, p. 42.

Cylindrophyllum Belanski, 1928, p. 176.

Type species.—*Cyathophyllum caespitosum* Goldfuss, 1826, p. 26.

Diagnosis.—Fasciculate colonial genus of the Disphyllidae characterized by radial septa in two orders, with monacanth septal trabeculae inclined inward from outer wall towards axis; septa with spindle-shaped dilation and with well-developed, globular dissepiments. Tabularium consists of flat, cap-like axial tabulae and peripheral, sagging tabulae.

Discussion.—The genus *Disphyllum* is a widespread

Middle and Upper Devonian rugose coral, belonging to the cosmopolitan faunas of that time. It is also the nominate genus of Hill's family Disphyllidae, and thus has an additional importance. Although the family Disphyllidae has been subdivided into four subfamilies by Hill (1981), I have elsewhere (1994, p. 333) pointed out problems with these subdivisions. The genus *Disphyllum* is central to the family and as nominate genus it must be clearly understood.

Most authors who have studied *Disphyllum* have agreed on its basic morphology. The inclined monacanth septal trabeculae, fusiform dilation of septa in the inner dissepimentarium, numerous rows of globular dissepiments and common occurrence of axial and peri-axial rows of tabulae in corallites with long septa are all accepted characteristics of the genus. Problems of nomenclature can arise when narrow dissepimentaria are developed, as these corals then may closely resemble species of the genus *Columnaria*.

Taxonomic difficulties have also resulted due to variation in colonial form. *Disphyllum caespitosum* occurs as both purely fasciculate colonies and also in more compact colonies which are indistinguishable (at least in part) from cerioid genera. Birenheide (1978, p. 90) stated that both cerioid and fasciculate, noncarinate corals of this group of the Disphyllidae should be placed in the genus *Disphyllum*. I suggested (1994, p.327) that *Disphyllum* should contain all those species that are dominantly fasciculate, accepting the tendency of some species to develop subcerioid colonies under certain environmental conditions. The problem does not arise in the Iowa faunas because both Cerro Gordo and Mason City beds contain only fasciculate colonies of *Disphyllum*.

A close relationship between some species of *Disphyllum* and species of the genus *Peneckiella* is indicated by a peripheral row of differentiated dissepiments present in some species, as in many colonies of *D. floydensis* and *D. iowense*, both described below. This is also distinctive in *D. fasciculum*, as identified by McLean and Sorauf (1989, p. 392). In both Iowa species there is a row of dissepiments in the periphery of the corallite which are uniformly larger and more bulbous than dissepiments internal to this row, and very commonly are thicker-walled than others. Especially in *D. iowense*, when there is a stereome coating forming a wall-like margin to the tabularium, the coating forms on the inner side of this row. In mature corals of these two species, there are always additional dissepiments interior to the peripheral row, but at one stage of corallite growth, there may be none. This feature is well illustrated in *D. fasciculum* (McLean and Sorauf, 1989, pl. 2, figs. 6,7), and also in specimens illustrated by Rohart (1988, pl. 35, figs. 10–13). This

feature led Rohart to place this coral species, from northern France, in the genus *Peneckiella*, but I would not regard the dissepiments in these individuals to be truly peneckielloid.

In addition to the four species of *Disphyllum* described here, a single colony of an additional species was collected from the Owen Member from the base of the uppermost stromatoporoid biostrome, at the Buseman Quarry south of Dumont, Iowa (Locality 40, Appendix). This single colony is similar to medium-sized species of the genus with long septa, but is not well enough preserved to warrant illustration here.

Disphyllum dispassum (Fenton and Fenton, 1924)

Plate 26, figures 3–10

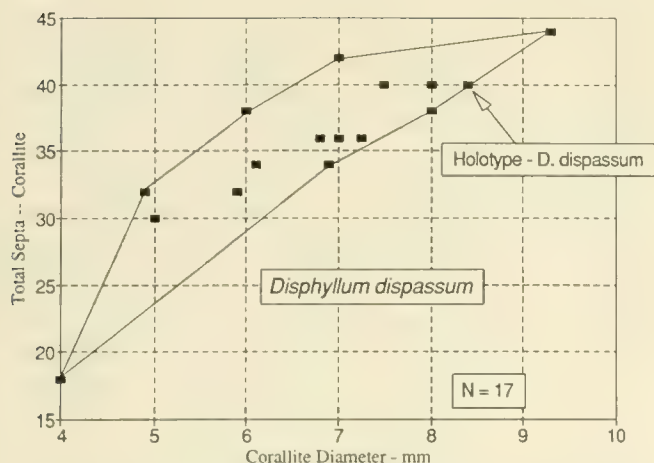
Heliophyllum dispassum Fenton and Fenton, 1924, p. 27, Pl. 10, figs. 4–8.

Disphyllum tubiforme Fenton and Fenton, 1924, p. 42, Pl. 2, figs. 1–4.

Diagnosis.—Small fasciculate colonies of *Disphyllum* with major septa of varying length, generally open tabularium with flat and complete or upbowed incomplete tabulae. Dissepimentarium narrow, with two or three rows of globular dissepiments most common, except where budding occurs in broadened dissepimentarium.

Description.—*Disphyllum dispassum* occurs as small colonies in the shaly rocks of the Cerro Gordo Member of the Lime Creek Formation. Some colonies are compact in their young stages, where rapid budding results in corallites commonly in lateral contact and prismatic, while generally in more adult (but still small) colonies, corallites are separate and truly fasciculate in form.

In transverse section, individual corallites are small, with a mean diameter of 7.4 mm for 12 mature-appearing corallites (range of 6.8 to 9.3 mm). These same corallites have a mean of 38.9 septa, (range of 36 to 44, Text-fig. 37). Septa are radially arranged, with clear differentiation into major and minor orders. The length of major septa varies, from short, extending at most $\frac{1}{2}$ way through the tabularium toward the axis, to long, in which major septa extend $\frac{5}{6}$ or $\frac{7}{8}$ way to the axis and swirl, so that there is only a very small open axial space. This variation is seen within individual colonies (Pl.26, figs.3,4,5,9), so that it cannot be used as a taxonomic character. The minor septa are almost invariably approximately one half the length of major septa, and are generally confined to the dissepimentarium. The dissepimentarium is narrow. Septal dilation is variable also, some with short and thin septa (Pl.26, fig.3) having weak, spindle-like dilation that only occurs in the outer tabularium. Other corallites have thicker septa which may be more heavily dilated



Text-figure 37.—*Disphyllum dispassum* from the Cerro Gordo Member, corallite diameter (in mm) plotted versus the total number of septa in individuals from six colonies studied. The holotype of the species is indicated on the graph.

in the outer tabularium (Pl.26, figs.7,9). Where septa are thin, their path in transverse section can be irregular, with septal trabeculae swollen somewhat to give a carinate-like appearance to them.

In longitudinal section, corallites commonly have a mostly open tabularium, with tabulae either complete and flat or arched, or incomplete and inclined. Where septa are long, there may be the development of typical disphyllid axial and peri-axial rows of tabulae. The dissepimentarium is generally narrow in this species, with two or three rows of globular, inclined dissepiments, expanding to many more rows of dissepiments prior to budding, which occurs in the outer dissepimentarium (Pl.26, figs.6,8).

Septal trabeculae are seen within septa in longitudinal sections. They incline adaxially at a rather uniform angle from the wall, generally about 50° to 55° from the vertical.

Type specimens.—Holotype FMNH 26045, paratype UMMP 7809. *Diphyphyllum tubiforme*, holotype FMNH 26014, paratypes FMNH 26015, UMMP 7853.

Discussion.—On the basis of external morphology, Fenton and Fenton proposed two species of fasciculate corals from the Cerro Gordo, *Heliophyllum dispassum* (1924, p. 27) and *Diphyphyllum tubiforme* (1924, p. 42), which are synonyms. They noted that *H. dispassum* had about 40 septa that “are strongly denticulate, and very heavy”, and that *D. tubiforme* has 40 to 46 septa, that “are strongly carinate”. The holotype of *D. tubiforme* was not sectioned; it does not have heavy or long septa (Pl.26, fig.4), and the Fentons’ sections of paratypes of both species are virtually identical. Both have moderately long septa that are thick. The only real difference between specimens in the type col-

lections is in colony form, as the holotype of *D. tubiforme* budded rapidly in its early stages of colony growth, thus, it is almost cerioid in the packing of juveniles around the parent. Fenton and Fenton noted that both species are variable in colony shape, and *D. dispassum* is indeed variable, both in colony shape and also in length and dilation of septa.

Disphyllum dispassum resembles *D. caespitosum*, as identified in the New York Frasnian fauna (Sorauf, 1987, p. 681). Both have long septa and three to four rows of dissepiments, with the outermost dissepiments larger and more bulbous than the rest, although the Iowa species has much less size and shape differentiation than does the New York form. Additionally, the septal trabeculae of *D. caespitosum* are much larger and more prominent than are those in *D. dispassum*. The Iowa species also is reminiscent of *D. fasciculum* in the differentiation of the outermost dissepiments, but the former has longer septa than does *D. dispassum* and only one or two rows of dissepiments.

Occurrence.—Specimens collected by Fenton and Fenton came from the “*Spirifer* zone” or upper Cerro Gordo Member at the Rockford Brick and Tile Quarry (Locality 35, Appendix), with the exception of one specimen of *D. dispassum*, UMMP 7809, which was collected from the upper part of the Cerro Gordo at Bird Hill (Locality 31). Specimens collected by me came from the South Portland locality (Locality 27) and the type Lime Creek (Locality 28). In both of these localities, the small, fasciculate colonies were collected approximately 4 m (12 to 13 ft) above the “rusty bed”. A single colony collected within the Cerro Gordo at Bird Hill (Locality 31) came from approximately 6.5 m (20 ft) below the base of the Owen Member. Colonies collected at the Rockford Brick and Tile Quarry (Locality 35) were all from material of the upper Cerro Gordo that had been stripped from underlying shales and left in dump piles.

***Disphyllum floydense* (Belanski, 1928)**

Plate 1, figure 3; Plate 27, figures 1–5; Plate 28, figures 1–4

Cylindrophyllum floydense Belanski, 1928, p. 176, Pl.12, fig.1.

Diagnosis.—Species of *Disphyllum* with colony mean diameter of tabularium between 4 and 5 mm., but with some colonies with larger diameters in southern part of outcrop area (6.4–10.7 mm). Long, straight major septa extend almost to corallite axis; fusiform dilation of both major and minor septa in the inner dissepimentarium somewhat variable in development. Dissepimentarium narrow, sometimes with only one row of elongate, almost peneckielloid dissepiments, but with as many as four or five rows of smaller, glo-

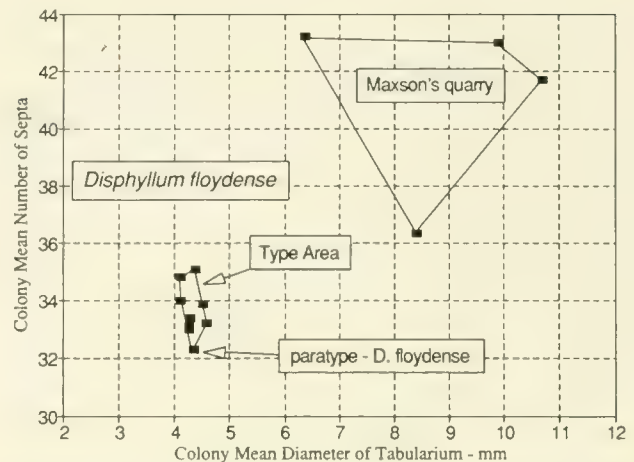
bose dissepiments. Tabularium characterized by axial series of flat-topped and periaxial series of sagging tabulae, usually interrupted in some parts of corallite by irregular inclined or incomplete tabulae.

Description.—*Disphyllum floydense* colonies are fasciculate; rapid offsetting forms compact branching colonies. Colony size is generally 25 to 30 cm in diameter (Pl.1, fig.1), with height being $\frac{1}{2}$ that dimension.

In transverse section, radially arranged septa are clearly organized into two orders, with major septa extending almost to the axis of the corallite, leaving approximately $\frac{1}{6}$ of the diameter of tabularium open at the axis, while minor septa extend only a very short distance into the tabularium (Pl.27, figs.1–4). Dilation of septa is fusiform, and in some corallites is extreme, with the periphery of the tabularium completely occupied by dilated septa (Pl.27, fig.2), while others are little dilated, occupying approximately $\frac{1}{3}$ to $\frac{2}{5}$ of this perimeter, averaging close to $\frac{1}{2}$ for the species. Mature corallites normally approximate 5.5 to 6.5 mm in total diameter, and tabularial diameters range from a colony mean of 4.1 in the smallest to 4.6 mm in the largest of the nine colonies studied from the type area (Text-fig. 38). In these same colonies, the mean number of septa ranges from 33.0 to 35.1. Colonies collected from the Nora Springs area to as far south as Cooper's Bend on the Shell Rock River are homogeneous in size and number of septa.

In longitudinal section the tabularium has an axial row of flat-topped, cap-like tabulae and a periaxial row of sagging partial tabulae (Pl.28, fig.2). This is typical of individuals with long, straight septa reaching almost, but not quite to the corallite axis. Where septa are shorter, or in corallites in which periodic differences in growth are seen, an irregular tabularium is developed, with incomplete tabulae, and with no axial series developed (Pl.28, fig.4).

The dissepimentarium is generally narrow, although this is variable. Where the dissepimentarium is narrow, there may be as few as one row of dissepiments. This single row is then composed of bulbous dissepiments, which may reach the epithecal wall and appear flattish in their peripheral portion. This form resembles that labeled "peneckielloid" by Hill (1981, p. F26, here shown in Pl.28, fig.2). Where the dissepimentarium is broad, generally two to four rows of small bulbous dissepiments are present, and these are more inclined axially at and near the boundary between the tabularium and dissepimentarium (Pl.28, fig.4). In several colonies the innermost row of dissepiments was coated by a layer of stereome, thus marking the inner boundary of the dissepimentarium. The dissepimentarium is generally wider when budding is taking place, as buds



Text-figure 38.—*Disphyllum floydense* from the uppermost beds of the Mason City Member, colony mean diameter of tabularium (in mm) plotted versus the colony mean number of total septa. The colonies from the type area, near Nora Springs south to Cooper's Bend, are uniform in their size and number of septa (including the paratype, as marked on the graph). Colonies from farther south, the Maxson Quarry at Marble Rock, Iowa, are markedly larger and more variable in numbers of their septa, but fit into the species in all other criteria.

arise from its outer portion. Then, six or seven rows of dissepiments may be present.

Septal structure is typical for the family, with monacanth septal trabeculae that are inclined adaxially. The angle the monacanth makes with the epithecal wall is 40° and this angle increases slightly near the inner dissepimentarium as the monacanth flex inward (Pl.27, fig.5). The trabeculae in this species of *Disphyllum* are large and rather feathery in appearance, as is common in the Disphyllidae. They become slightly larger in some corallites, which then have a knobby appearance in transverse section. This "carinate" condition (Pl.27, fig.4) is never uniformly developed in corallites of this species.

Type specimens.—Holotype SUI 2001, paratypes SUI 364, 753, and 2003, and USNM 71029, UCM 1477.

Discussion.—In addition to abundant colonies noted in the type area of the species (from Nora Springs to Cooper's Bend), four additional corals have been collected from Maxson's Quarry at Marble Rock (Locality 24, Appendix), far to the south of the southernmost occurrences in the type area. The species is homogeneous near Nora Springs, displaying little tendency to develop larger corallites. The four colony sample from Marble Rock (Maxson's Quarry) contains one very large form, with a mean diameter of 9.9 mm for nine corallites, and 43 as the mean number of septa (Text-fig. 38); a second large-diameter colony, with mean

diameter of 10.7 mm and mean number of septa of 41.7 for five corallites, and two other colonies which are a more normal size for the species, with mean diameters of 8.4 and 6.4 mm, and 36.3 and 43.6 mean septa. The very large corallites in the two colonies are larger than for any of those collected near Nora Springs, and the remaining colonies from Marble Rock are nearly intermediate in size to those in the type area. The corallites are like those of *Disphyllum floydense* from the type area in every other way but size and number of septa in the few large corallites (Pl.28, fig.3).

In longitudinal section, the specimens from the southern area also show the common development of a row of large to very large dissepiments in the peripheral portion of the dissepimentarium (Pl.28, fig.4). These dissepiments are not as uniform in size, nor is the outermost row as uniform in development or as well-differentiated from other, more inclined dissepiments, as are those of *D. conjugens* n. sp., or *D. iowense*, both described below. Nevertheless, there appears to be a relationship between these three species, the two from the upper Mason City Member, the other from the Nora Member.

Disphyllum fasciculum (Meek, 1877) is close to *D. floydense* in appearance, with its long, straight major septa, fusiform septal dilation, and narrow tabularium. Stumm (1940, p. 62) noted that *D. fasciculum* has corallite diameters of 5 mm and septal numbers of 34 to 36, thus, with respect to these parameters, the species are very similar. Stumm also noted that the minor septa are extremely short, "never extending more than 1 mm from the periphery" (1940, p. 63). On the same page he also said that the species is characterized by a single row of dissepiments in the narrow dissepimentarium, which can sometimes be the case in some corallites in *D. floydense*. The specimen labeled *Disphyllum fasciculum* illustrated by McLean and Sorauf (1989, p. 392) from the Twin Falls Formation of western Canada is very close in the appearance of its septal dilation, dissepimentarium, and tabularial configuration to *D. floydense*, but the size is larger, with corallite diameters from 9 to 11 mm (measured from photographs), and with septal numbers ranging from 38 to 40, which resemble the largest specimen collected from Maxson's Quarry as discussed above, and suggests that the two species are very closely related (or perhaps should not be separated).

Disphyllum floydensis resembles the Frasnian species *D. caespitosum* (as illustrated in Sorauf, 1987, fig. 7.1) in that both have long septa, both have a well-differentiated external row of bulbous dissepiments, and both have large septal trabeculae. Septal dilation in *D. floydensis* is much greater than in the New York

specimens, however, and in fact, is greater than in other North American species with long septa, except for *D. densum* (Smith, 1945, p. 22). *Disphyllum densum*, when restudied, may be found to be a junior synonym of *D. floydensis*.

Occurrence.—*Disphyllum floydensis* was reported by Belanski (1928, pp. 344, 346) from the uppermost "soft, yellow, argillaceous limestone" of the Mason City Member at its type section, and from the type section of the Rock Grove Member. In his collection, there is also a specimen from "Belanski's Quarry" in Nora Springs, near the old mill dam. The Nora Dam locality yielded numerous specimens (Locality 8, Appendix), while a few colonies were collected at Cooper's Bend on the Shell Rock River north of Rockford, Iowa (Locality 19) and from Maxson's Quarry near Marble Rock (Locality 24). In each case, the occurrence of this species was from the uppermost beds of the Mason City Member.

***Disphyllum conjugans*, new species**

Plate 1, figure 5; Plate 28, figures 5–7; Plate 29, figures 1,2

Diagnosis.—Small diameter species of the genus with long major septa nearly reaching to axis of corallites, with long minor septa, about $\frac{1}{2}$ length of major, and extending into tabularium. Heavy septal dilation in dissepimentarium, with single row of uniformly large flattish but globular dissepiments coated with stereome and with two to four additional rows of inclined dissepiments interior to peripheral row. Tabulae differentiated into uniform cap-like, flat-topped axial row and sagging periaxial rows.

Description.—*D. conjugans* generally occurs as small colonies, but of four samples available, three were of broken and/or stromatoporoid coated corallites in the Nora biostromes, so that it is not possible to give colony mean dimensions.

In transverse section, these corals are marked by long major and long minor septa. The major septa reach to, or almost to, the corallite axis, and some join laterally. Major septa are usually greatly dilated in the inner dissepimentarium, and may maintain their maximum width to the epithecal wall or thin somewhat in the outer dissepimentarium (Pl.28, figs.5,6). The major septa thin rapidly in the tabularium and are straight, not swirled in the axial area. Minor septa are long, generally reaching $\frac{1}{2}$ as far as major septa into the tabularium. Corallites are large, ranging up to 8 mm in outer diameter with 34 to 43 septa. In three specimens, corallite diameters ranged from 5.7 to 8.0 mm, with a mean of 6.8 for nine corallites and septa numbered from 34 to 36 with a colony mean of 35.8 in the first specimen; diameters ranged from 5.8 to 7.5

mm in seven corallites, with a mean of 6.6 mm, and with septa ranging from 36 to 38, with a mean of 36.7 in the second specimen. In the third and largest colony, diameters ranged from 5.6 to 7.8 mm, with a mean of 6.8 mm for six corallites, while septa numbered from 40 to 42, with a mean of 40.7. These samples are discussed as three colonies, but in reality, since corals are fragmented and loose in matrix, one cannot prove that only three colonies are involved. Each sample, however, seems to be internally consistent in size and number of septa. Thus, the species has medium large corallites, with a correspondingly large number of septa. There is a solid wall of dilated septa and biogenic stereome surrounding the tabularium, and the species is distinctive. In transverse section a single row of large dissepiments is also seen in an oblique portion of the peripheral part of the dissepimentarium (Pl.28, fig.5).

In longitudinal section, one of the most distinctive features of this species is the row of large, flattened, globular dissepiments at the periphery of corallites (Pl.29, fig.2). Dissepiments in this row are thicker-walled than other dissepiments, are considerably larger, and are stacked in a uniform row. Thinner-walled, inclined globular dissepiments are present inside this single row, occurring in one to four rows lining the margins of the tabularium. Ordinarily, the species has only one or two rows of these internal dissepiments. Tabulae are differentiated into axial and periaxial rows, with axial tabulae being flat-topped, cap-like structures accompanied by uniformly sagging periaxial tabulae. This configuration is similar to that in many species with long septa in this family, and occurs in several genera. Septal trabeculae are flat, lath-like monacanthi which make a considerable angle to the outer wall. In one specimen an angle of 60° from the vertical was measured, and trabeculae generally bend inward to approach horizontality in the innermost dissepimentarium.

Type Specimens.—Holotype SUI 1625, paratypes SUI 1624, 1376.

Discussion.—This is a distinctive species of *Disphyllum* based on the extreme development of bulbous and thickened dissepiments at the periphery of a relatively broad dissepimentarium. This is apparently coupled with marked septal dilation in the dissepimentarium, especially in its outer part. Where septa are less dilated, there still may be a solid sleeve around the tabularium of the corallites, as stereome is deposited on the inner side of these large peripheral dissepiments. Although these dissepiments are not truly peneckielloid, they do indicate a relationship to the other Mason City species, *D. floydense*, and also to the widespread *D. fasciculum*, known from the Frasnian of western Canada and *Peneckielia fascicularis* (Soshki-

na), from France (Rohart, 1988). The appearance of the latter strongly suggests that it is a species of *Disphyllum* with strongly differentiated outermost dissepiments and several additional rows of more axial normal dissepiments that are strongly inclined axially (Rohart, 1988, pl. 35, figs.10,11). The complex of species with long septa and differentiated, bulging peripheral dissepiments need to be restudied in order to clarify relationships between *Disphyllum* and *Peneckielia*.

Corals discussed here came from both the upper and lower biostromes of the Nora Member. Two colonies from the upper biostrome at County Roads Quarry (Locality 14) are approximately the same diameter, with colony means of 37 and 36 septa, while a third colony, from the lower biostrome at Reed Creek (Locality 4), has a colony mean of 41 septa. In other respects, all three are closely similar, although one of the colonies (from Locality 14) has greater development of internal dissepiments, with as many as four rows of these inclined dissepiments.

Occurrence.—The three colonies available were collected from two localities, with the two having somewhat smaller diameters being from the upper biostrome of the Nora Member at the County Roads Quarry (Locality 14, Appendix), while the colony with slightly larger corallite diameters was collected from the lower Nora biostrome at Reed Creek (Locality 4).

***Disphyllum iowensis*, new species**

Plate 1, figure 4; Plate 29, figures 3–9

Diagnosis.—*D. iowensis* is a large diameter species of the genus with relatively few, short, slender septa, with major septa reaching $\frac{2}{3}$ of the way to the axis and minor septa only $\frac{1}{2}$ to $\frac{1}{3}$ as long as major septa. A narrow dissepimentarium is filled with steeply inclined, elongate dissepiments, and tabularium with complete tabulae only in axial area.

Description.—The four specimens examined are complete colonies; three are small, with only three to four corallites, and the other is larger, with 15 to 17 corallites preserved (although crushed and broken internally). The larger colony has closely packed corallites, but none have adopted the prismatic shape characteristic of a cerioid colony.

In transverse section, diameters range from 9 to 15 mm, and the largest corallite has 44 septa, although 42 is normal. Major septa are relatively short, extending $\frac{1}{2}$ to $\frac{2}{3}$ of the way from its periphery to the corallite axis. Septa are relatively slender, are dilated to about twice normal width in the dissepimentarium of the smaller colony, but remain slender throughout corallites of the larger colony (Pl.29, fig.3). Minor septa are very short, restricted to the narrow dissepimentarium,

with total length only about $\frac{1}{2}$ that of major septa, and they remain slender. Because of the delicacy of the corallites and their slender septa, much breakage occurred due to compaction and diagenesis. The intersection of septa with tabulae indicates that septa do interfere with formation of tabulae, as segments of tabulae intersect septa and are straight in the tabularium. In smaller colonies, the outermost part of the tabularium and dissepimentarium are characterized by heringbone dissepiments (Pl.29, fig.7).

In longitudinal section, the tabularium has flat or irregular, complete tabulae only in the axial portion of the tabularium. Peripherally the tabularium is filled with disrupted tabulae that remain fragmental between septa. The dissepimentarium has five to six rows of steeply inclined, globose, elongated dissepiments in mature corallites, commonly having large dissepiments close to the epithecal wall. In youthful colonies corallites at first have no dissepiments, then one row of bulbous dissepiments adjacent to the wall, and then they add additional internal, inclined dissepiments around the tabularium margin (Pl.29, fig.6).

Type Specimens.—Holotype SUI 541, paratypes SUI 1509, 1626 and 1756.

Discussion.—*Disphyllum iowense* belongs to the group of species that are marked by the presence of bulbous peripheral dissepiments (as are *D. floydense* and *D. conjugans* discussed above). It is also characterized by its large septal trabeculae which can be swollen, giving it a carinate-like appearance, as common in many species of *Hexagonaria*, and marked septal dilation in the dissepimentarium. Septa are variable in length, but in three of the four colonies studied here a wide area remains open in the axial part of the tabularium.

D. iowense resembles *D. fasciculum* (Meek, 1877) in its peripheral dissepiments, although the latter (as illustrated by McLean and Sorauf, 1989, Pl.2, figs 6,7) has a smaller diameter and contains fewer septa than does the Iowa species. *D. fasciculum* is a widespread North American species which probably has numerous synonyms, but at present it is not known exactly how widespread or how many species should be regarded as its synonyms. The Iowa species also has a resemblance to *D. caespitosum* that is common in European Frasnian strata in that the latter likewise has peripheral bulbous dissepiments. As illustrated by Rozkowska and Federowski (1972, p. 317), *D. caespitosum* contains a significantly larger number of normal, axially inclined dissepiments. Other species with peripheral bulbous dissepiments are *D. rugosum*, *D. kostetskae* and *D. fascicularis* (Soshkina), all of which have been recognized in Frasnian rocks of Belgium (Tsien, 1970), with the latter two first described from Russia (Soshkina, 1949, 1952).

D. iowensis is differentiated from these three species either by degree of septal dilation or because of abundance of dissepiments.

Occurrence.—All specimens of *D. iowense* are from the top feet of the Mason City Member, the holotype collected at Baumgardner's Mill (Locality 17, Appendix), the paratypes at Belanski's locality 38, which is an abandoned quarry in the southern part of Nora Springs (Locality 11, Appendix).

Genus *HEXAGONARIA* Gürich, 1896

Hexagonaria Gürich, 1896, p. 171; Hill, 1956, p. F280; Sorauf, 1967, p. 24; Pickett, 1967, p. 25; Birenheide, 1969a, p. 41; Tsien, 1977, p. 208; Birenheide, 1978, p. 87; Hill, 1981, p. F275; Rohart and Semenov-Tian-Chansky, 1981, p. 4; Rohart, 1988, p. 267; Sorauf, 1988, p. 168; Wrzolek, 1992, p. 237; Sorauf, 1994, p. 332.

Argutastrea Crickmay, 1960, p. 10; Hill, 1981, p. F266.

Pseudohexagonaria Krämer, 1982, p. 654.

?*Cystihexagonaria* Rohart, 1988, p. 273.

not *Pseudohexagonaria* Coen-Aubert and Lutte, 1990, p. 23.

not *Argutastrea* Coen-Aubert and Lutte, 1990, p. 20.

Type Species.—*Cyathophyllum hexagonum* Goldfuss, 1826, by subsequent designation (Lang et al., 1940, p. 69).

Diagnosis.—Cerioid colonial corals of the Disphyllidae, with clear differentiation of the tabularium and dissepimentarium, thus, also the calicinal platform and axial pit. Long major septa extend well into the tabularium although shorter minor septa do not, and septal dilation is spindle-shaped, with maximum dilation in the inner dissepimentarium. Interference of (usually) long septa with tabulae commonly, but not always, results in development of axial and periaxial rows of tabulae. Septal monacanth trabeculae of disphyllid, lath-like type show sharp boundaries with one another in longitudinal view. The dissepimentarium contains numerous globose dissepiments (generally five to ten per row). Where dissepimentarium is wide, outer dissepiments approach horizontality, but inner dissepiments are always steeply inclined towards the corallite axis. Septal trabeculae seen in longitudinal section form a structure that reflects the orientation of dissepiments; thus are perpendicular to calicinal surfaces. As a result they form either a uniformly inclined cluster of trabeculae or a splay of trabeculae with axial inclination that increases to the innermost part of the dissepimentarium where bending occurs. Reflexing of calicinal platform and rows of dissepiments can result in the formation of upwardly bowed rows of dissepiments and accompanying upward divergence of septal trabeculae.

Discussion.—*Hexagonaria* is a common and widespread genus, and has been described or reported by numerous authors from many horizons in many parts of the world. The synonymy given above is not com-

prehensive; the reader is referred to Birenheide (1969a) or Hill (1981) for more complete synonymies. The genus has been variously defined; as a result a number of generic names have been proposed for some of the species that should be included within *Hexagonaria*. I have elsewhere (Sorauf, 1994, p. 327) provided an extended discussion of the genus name usage, varying definitions of the genus, various interpretations of the type specimens of *Hexagonaria hexagona*, as well as the resulting multiplicity of interpretations of the genus, and the effects of this on genus, subfamily and family nomenclature for species. Varying diagnoses for this genus have resulted in a great deal of confusion about some other colonial genera of the Disphyllidae.

Much of this confusion has resulted from the presence of carinae-like septal structures in the neotype and topotypes of *Hexagonaria hexagona* from Frasnian strata in the Refrath area of northwestern Germany. Pickett (1967, p. 59) chose a neotype for the species, and his choice has been followed by all subsequent workers. This, and other topotypic specimens have septa with laterally expanded septal trabeculae which resemble septal carinae. I have shown (Sorauf, 1994, p. 332) that this expansion is part of the process of septal dilation, and pointed out that not all corallites have this feature fully developed in the type specimen. I concluded that it is an error to exclude colonial disphyllid corals lacking such structures from the genus. Wrzolek (1992, p. 237) has also recognized that septal "carination" is often weakly or sporadically developed in *H. hexagona* and recognized a separate subspecies for a population of the species from the Holy Cross Mountains of Poland. Hill had characterized the genus (and its subfamily) as having "typically closely carinate septa with predominantly yardarm carinae" (1981, p. F275). In so doing, she followed Birenheide (1978, p. 95), whose opinion was that the genus name should be exclusively applied to cerioid coral colonies with yardarm carinae. I regard the "carinae" seen in the type species of the genus, and other closely related species, as dissimilar to yardarm carinae as developed in *Heliophyllum* and related genera (Sorauf, 1994, p. 326). Part of my understanding of this variable development of septal structures is based on study of the Iowa species *Hexagonaria bassleri* and *H. oweni*, both of which have variable dilation of septa trabeculae and variable development of yardarm-like septal structures.

The genus name *Hexagonaria* is used here to include species with typically dilated septa which may or may not bear weakly or strongly developed carinae-like septal structures. More briefly stated, it is used to include generalized cerioid colonial corals of the family Disphyllidae. The genera *Pseudohexagonaria* Krä-

mer, 1982 and *Argutastrea* Crickmay, 1960 are synonyms in that they were first defined as pertaining to *Hexagonaria*-like corals lacking carinae. These two genera, as redefined by Coen-Aubert and Lutte (1990, pp. 20,23) retain their usefulness. Neither pertains to the Frasnian species in Iowa, which are rather central to the genus concept of *Hexagonaria*, as typified by *H. hexagona*. The genus *Cystihexagonaria* Rohart, 1988, proposed for *Hexagonaria*-like corals with limited development of a lonsdaleoid dissepimentarium, may be of use in dealing with some species, but has no applicability to species from Iowa.

***Hexagonaria bassleri* (Webster and Fenton,
in Fenton and Fenton, 1924)**

Plate 3, figure 7; Plate 30, figures 1–6; Plate 31,
figures 1–6; Plate 32, figures 1–5; Plate 33, figure 1

Acervularia bassleri Webster and Fenton, in Fenton and Fenton, 1924, p. 58, Pl. 13, fig. 2, Pl. 14, figs. 4–6.

Acervularia bassleri depressa Webster and Fenton, in Fenton and Fenton, 1924, p. 60, Pl. 12, figs. 1,2.

Acervularia bassleri magna Webster and Fenton, in Fenton and Fenton, 1924, p. 61, Pl. 14, fig. 6.

Prismatophyllum cf. *P. magnum* Smith, 1945, p. 47, Pl. 15, figs. 1–4, Pl. 18, fig. 2.

Prismatophyllum reticulatum Smith, 1945, p. 48, Pl. 16, figs. 1–3, Pl. 18, fig. 4; McLean, 1984, p. 472.

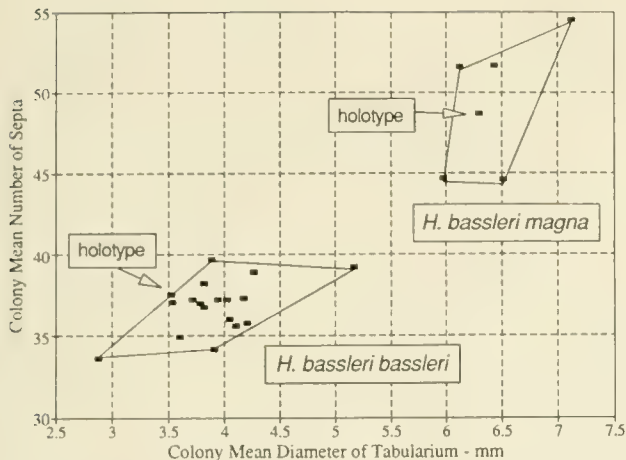
Hexagonaria bassleri McLean, 1984, p. 472; McLean and Sorauf, 1989, p. 394, Pl. 2, figs. 1,2; Sorauf, 1994, p. 332, Pl. 2, figs. A–F, Pl. 3, figs. A–D.

Hexagonaria magna McLean, 1984, p. 472.

Hexagonaria bassleri magna McLean and Sorauf, 1989, p. 383

Diagnosis.—Species of *Hexagonaria* with wide range of corallite size and septa numbering from 30 to 40, clearly differentiated into major and minor. It resembles the type species of the genus, *H. hexagona*, in shape of septa in transverse section and occasional development of swollen septal trabeculae and resultant carinae-like structures. Tabularium displays both flat-topped axial row of tabulae and periaxial sagging tabulae; dissepimentarium filled with small dissepiments.

Description.—*H. bassleri* occurs in flattened cerioid colonies with dimensions generally approaching 20 cm in diameter and 10 cm in thickness. Corallites show a great range in size, with the colony mean diameter of tabularium varying from 2.9 to 7 mm, and the colony mean number of septa varying from 34 to 55. These numbers are deceptive, however, because the core group of *H. bassleri* varies only from 4 to 6.5 mm in mean colony tabularium diameter and from 34 to 45 in colony mean septa (Text-fig. 39). The larger form (Pl. 32, fig. 2) is sufficiently different to warrant the use of the subspecies name *H. bassleri magna*, proposed by Webster and Fenton, and the single small specimen is the holotype of a small subspecies named *H. bas-*



Text-figure 39.—*Hexagonaria bassleri* from the upper part of the Owen Member, the so-called “*Acerularia* zone”, colony mean diameter of tabularium (in mm) is here plotted versus the colony mean for the total number of septa. The typical subspecies is smaller, with fewer septa than the larger subspecies *H. bassleri magna*, recognized by Webster and Fenton in 1924.

sleri depressa by Webster and Fenton, but not recognized here.

In transverse section two phenotypes are noted. The first is represented by the holotype and by the majority of colonies in the sample. Here, septa are thin in the outer dissepimentarium and are dilated, with typical spindle-shaped dilation in the inner dissepimentarium. Major septa then taper to be thin and blade-like, continuing into the tabularium, where they reach nearly to the corallite axis and are deflected to swirl slightly around the small open space at the axis (Pl.30, figs.1,6). The diameter of the axial open space is approximately $\frac{1}{6}$ the tabularium diameter or less. The other form occurring here is seen in one of the paratypes and occasionally elsewhere. In these colonies, septa are heavier, and septal dilation is more spear-shaped in the inner dissepimentarium, with the heavy dilation continuing into the outer tabularium (Pl.31, fig.4). In fact, the widest part of the septa is in the outer tabularium. The heavy septa commonly have swollen trabeculae in the outer dissepimentarium, and bear structures resembling carinae in some corallites. Some corallites, especially immature ones, have major septa that extend to the axis where they swirl or connect irregularly across the axis.

In both forms, the inner dissepimentarium is marked by closer spacing of dissepiments, as the section plane cuts more steeply inclined dissepiments that surround the outer tabularium. The outer dissepimentarium has more widely spaced intersections, interseptal spaces can be very large in the outer corners of asymmetrical corallites, and septa may even be somewhat discontin-

uous here. This incompleteness of septa and associated(?) large dissepiments may be related to the budding process, as suggested by the location of the areas affected (Pl.30, fig.2; Pl.32, fig.1).

In longitudinal section, all corals of the species have the type of tabularium characteristic of species of *Hexagonaria* with long major septa, thus have an axial row of flat-topped, cap-like tabulae and periaxial rows of uniformly downbent tabulae or more rarely, flat or inclined straight tabulae (Pl.30, figs.3,5). This shape of tabularium is characteristic of many species in the Disphyllidae. The dissepimentarium is also typical of the family in that it consists of rows of uniformly-sized dissepiments that are steeply inclined next to the tabularium, and are flat near the outer wall. Generally there is a rather uniform change of slope from steeply inclined near the tabularium to flat near the wall, but this may vary, and even show some arching as a result of reflexing of the calicinal platform.

Septal fine structure is clearly seen in longitudinal sections, and trabeculae are characteristically rather large, well-defined monacanthi that are sometimes somewhat swollen and feathery in appearance. The monacanthi make a small angle with the outer wall of the corallite, and bend progressively inward to make an angle approaching 45° in the inner dissepimentarium, where they commonly flex inward to be almost horizontal in the outer tabularium (Pl.31, figs.5,6).

Type specimens.—Holotype USNM 78619, paratypes USNM 78621, UMMP 8085. *H. bassleri depressa* holotype USNM 78620, paratype UMMP 8084.

Discussion.—Numerically, this species dominates the uppermost beds of the Owen Member of the Lime Creek Formation. It is very typical of the genus *Hexagonaria*; in fact, I regard it as closely related to *Hexagonaria hexagona* (Goldfuss) (see Sorauf, 1994, p. 332). As a species with long septa, it exhibits axial and periaxial rows of tabulae, and very typical spindle-shaped septal dilation is seen in transverse section. In addition, this species of *Hexagonaria* resembles the type species in that both have characteristic inflation of septal trabeculae as part of the septal dilation process. *H. bassleri* shows a range of septal thicknesses, from virtually undilated, through partly dilated with swollen septal trabeculae, to heavy, dilated septa with trabeculae swollen to form “carinae” (Pl.31, figs.1–4). Although these swollen septal trabeculae may be legitimate septal carinae, they are not analogous to the yardarm carinae formed in *Heliophyllum* and other genera, where carinae are formed prior to the infilling of interseptal spaces of the septa and are not part of a process of septal dilation. For this reason, the carinate structures of *Hexagonaria* are here referred to as “carinae” or “carinae-like structures”. Septal carination, its

description, and understanding of its construction and function are vital to the proper evaluation of the genus and the family Disphyllidae (Sorauf, 1994, p. 333).

In addition to showing variation in septal dilation and carination, *H. bassleri* also shows considerable variation in size as measured by diameter of tabularium; and number of septa (Text-fig. 39). The distribution of colonies by mean size and septal number indicates that Webster and Fenton were correct in recognizing a large subspecies of *H. bassleri*, *H. bassleri magna* (in Fenton and Fenton, 1924, p. 61). In addition to the holotype, a number of very large diameter colonies were collected at the Lillibridge Quarry (Locality 38, Appendix). This subspecies is described below.

Occurring alongside this subspecies with large corallites are much more numerous colonies of normal size (Text-fig. 39). These corals were also collected from the same uppermost beds of the Owen Member, at Owen Grove and all other localities where the unit outcrops or is quarried. This normal-sized group includes the holotype; thus I recognize the subspecies, *H. bassleri bassleri* Webster and Fenton, in Fenton and Fenton, 1924, p. 58. This is the nominate subspecies, as a result of change in rank; there is no change in authorship or date.

Webster and Fenton also proposed a subspecies, *H. bassleri depressa* for colonies of the species with smaller corallites. They emphasized the depth of the calicinal pit, but I consider this feature too much affected by growth stage, ecologic conditions and preservation to be a practical taxonomic criterion. The size of corallites in the holotype of the *depressa* subspecies is indeed small, but not much smaller than in the holotype of the species, and their subspecies paratype (UMMP 8084) has a larger colony mean corallite size than many other coralla of the species. This subspecies is here regarded as a synonym of the nominate subspecies.

H. bassleri resembles a number of described Frasnian species of the genus from Belgium and the Boulonnais Region of north France. These all are characterized by long major septa that reach to, or almost to, the corallite axis, have spindle-shaped septal dilation, and thin septa in the dissepimentarium with numerous globular dissepiments occurring in rows steeply inclined at the boundary between the tabularium and dissepimentarium, and which have axial and peri-axial rows of tabulae. This list includes the following species: *H. marmini* (Rohart, 1988, p. 268) and *H. mae* (Rohart, 1988, p. 270) from the Frasnian of north France; *H. buxutiensis* (Tsien, 1977, p. 213), *H. mae* and *H. gamboni* (Tsien, 1977, p. 215; Coen-Aubert, 1979, p. 11), and *H. mirabilis* (Coen-Aubert, 1979, p. 6) from the Frasnian strata of Belgium. The relation-

ships between the *H. bassleri* group in Iowa and western Canada to these numerous species in Europe remain to be established.

H. bassleri is regarded as senior synonym of *H. reticulata* (Smith) by McLean (1984, p. 472). Smith (1945, p. 48) described *Prismatophyllum reticulatum* from Frasnian beds in the Northwest Territories of Canada. I have not seen the types of this species.

Occurrence.—*H. bassleri* was listed by Fenton and Fenton (1924, p. 59) as present throughout the Owen Member, and especially common in the uppermost beds, their "Acervularia zone". I collected this species at both Owen Grove and Owen Grove West (Localities 25 and 26, Appendix), and at quarries in the Owen Member at Rockwell, Iowa (Locality 36) and at Lillibridge Farm (Locality 38), and at localities 40, 40A and 41, south of Dumont, Iowa. In all cases but one, the unit containing *Hexagonaria bassleri* was the uppermost limestone bed of the Owen Member (the "Acervularia zone" of Fenton and Fenton). At the quarry on the Carrollus Farm (Locality 41), a single specimen of *H. bassleri* was collected from low in the Owen Member, approximately 2 m above the basal limestones containing branching stromatoporoids. Thus, the local range zone for this species extends through most of the Owen Member.

***Hexagonaria bassleri bassleri* (Webster and Fenton, in Fenton and Fenton, 1924)**

Plate 3, figure 7; Plate 30, figures 1–6; Plate 31, figures 1–6; Plate 32, figure 1

Acervularia bassleri Webster and Fenton, in Fenton and Fenton, 1924, p. 58, Pl. 13, fig. 2, Pl. 14, figs. 4, 5.

Acervularia bassleri depressa Webster and Fenton, in Fenton and Fenton, 1924, p. 60, Pl. 12, figs. 1, 2.

Hexagonaria bassleri bassleri McLean and Sorauf, 1989, p. 388, Pl. 2, figs. 1, 2.

Diagnosis.—As for the species, excluding large diameter subspecies described under *H. bassleri magna*.

Type Specimens.—As for the species, holotype USNM 78619, paratypes USNM 78621, UMMP 8085.

Discussion.—Although Webster and Fenton did not formally propose a nominate subspecies for *Acervularia bassleri*, but did propose the subspecies *Acervularia bassleri magna*, they in essence, created the subspecies *A. bassleri bassleri* by removal of those coralla characterized by large corallite sizes. I accept both as legitimate subspecies of *Hexagonaria bassleri*. The subspecies *Acervularia bassleri depressa*, proposed by Webster and Fenton, in Fenton and Fenton, 1924, p. 60, is properly regarded as part of *Hexagonaria bassleri bassleri*.

Occurrence.—As noted above, this subspecies is present at all outcrops yielding the species. Only those

localities listed under *H. bassleri magna* contain the other subspecies.

Hexagonaria bassleri magna (Webster and Fenton,
in Fenton and Fenton, 1924)

Plate 32, figures 2–5; Plate 33, figure 1

Acervularia bassleri magna Webster and Fenton, in Fenton and Fenton, 1924, p. 61, Pl. 14, fig. 6.

Hexagonaria bassleri magna McLean and Sorauf, 1989, p. 383.

Hexagonaria magna McLean, 1984, p. 472.

Prismatophyllum cf. *P. magnum* Smith, 1945, p. 47, Pl. 15, figs. 1–4, Pl. 18, fig. 2.

Diagnosis.—*Hexagonaria bassleri* with large corallites, large diameter of tabularium, and numerous septa.

Description.—Coralla of this subspecies are not noticeably larger than others of the species, but contain fewer, larger corallites than the nominate subspecies. Corallites of *H. bassleri magna* are large, with their diameter of tabularium varying from 6 to 7 mm, with a mean of 6.5 mm for the six colonies studied (Text-fig. 39). Their septa are more numerous than others in the species, with colony means of from 49 to 55, with a mean of 52. In other respects the subspecies is similar to others included in *H. bassleri*.

Type Specimen.—Holotype USNM 78637.

Discussion.—*H. bassleri magna*, considered here as a valid subspecies, has been recognized in western Canada (Smith, 1945; McLean, 1984; McLean and Sorauf, 1989). It has been regarded as a species by Smith and a subspecies of *H. bassleri* by other authors. In the Iowa fauna this form with large corallites appears to me to be clearly separable only on the basis of corallite size, and I do not consider it a separate species.

This taxon is similar to Frasnian species of western Europe that have long septa and large corallites. In size of corallites, it resembles *H. hexagona* (Goldfuss, 1826), but contains many more septa than does this German form (Sorauf, 1994).

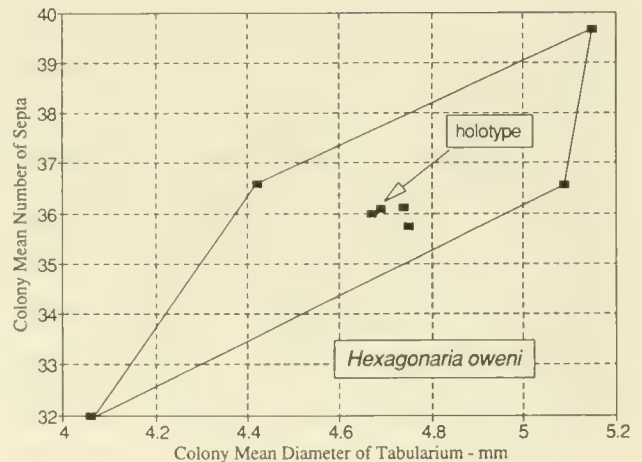
Occurrence.—The holotype was collected from Owen Grove, from the uppermost beds of the Owen Member, from the “*Acervularia* zone” of Fenton and Fenton (1924, p. 8). Further specimens were collected by me from these same beds at the Lillibridge Quarry (Locality 38, Appendix).

Hexagonaria oweni (Belanski, 1928)

Plate 1, figure 7; Plate 33, figures 2–5; Plate 34,
figures 1, 2

Prismatophyllum oweni Belanski, 1928, p. 174, Pl. 1, fig. 2.

Diagnosis.—Species of *Hexagonaria* with medium to small corallites characterized by long major septa that are very thin in the tabularium, with small open axial space. Tabularial diameter has a small range (4



Text-figure 40.—*Hexagonaria oweni* from the upper biostrome of the Nora Member, colony mean diameter of tabularium (in mm) plotted versus the colony mean for total number of septa in each corallite.

to 5 mm), and while major septa always dilate, minor septa commonly do not. Occasional “carination” of septa occurs in some colonies, but small diameter corallites have stout, smooth septa.

Description.—*H. oweni* occurs in flattened, discoid colonies with maximum diameters commonly approaching 20 cm and height approaching 10 cm. Corallites are relatively small, and colony means for the tabularial diameter vary from 4 to 5 mm, a narrow range of variation (here for eight colonies), and colony means for the septal number vary from 32 to 40, as diameters increase (Text-fig. 40). The size of tabularial diameter and the number of septa are closely correlated in this species. Septa occur in two orders, and major septa extend into the tabularium as thin, blade-like extensions to the axial area, where a small open space remains with its diameter $\frac{1}{4}$ to $\frac{1}{5}$ of the tabularium. In some colonies, some corallites have long major septa which join at the corallite axis. Septal dilation is marked, especially in major septa, as minor septa can remain undilated. In many colonies, especially those with small corallites, septa are stout in the outer dissepimentarium, have marked dilation in the inner dissepimentarium and rapidly taper to thin blades in the tabularium. Septal trabeculae are expanded to form “carinae-like” structures in some corallites (Pl. 34, fig. 2). In the colony with smallest corallites, the short, stout septa do not bear “carinae”. Here, intercorallite walls have a zigzag path in transverse section, caused by the position of septa being offset between neighboring corallites (resulting in the zigzag path). In colonies with larger corallites, septa are thin in the outer

dissepimentarium and corallites have straight intercorallite walls.

In longitudinal section the tabularium has an axial series of flat-topped, cap-like tabulae and a periaxial row of sagging tabulae, or irregular, complete tabulae. In those colonies with short major septa, tabulae tend to be more complete and differentiation into axial and periaxial rows disappears (Pl.34, fig.1). The dissepimentarium is filled with five or more rows of dissepiments, which vary in size, from small and globular to more elongate and larger. Rows of dissepiments tilt axially as they progress into the inner dissepimentarium, and the innermost rows are tilted nearly 90°, lining the tabularium.

Septal trabeculae are well-differentiated, large monacanth, as is typical for the genus. Trabeculae form a small angle (<30°) with the corallite wall and bend inward, and then flex inward to near horizontal at the outer boundary of the tabularium (Pl.34, fig.1).

Type Specimens.—Holotype SUI 471, paratypes SUI 134, 1522, USNM 71041, UCM 1474 (last specimen not seen).

Discussion.—This species shows its close relationship to *H. hexagona* by its long major septa, axial and periaxial rows of tabulae, occasional “carination”, and broad, well-differentiated monacanthine septal trabeculae which flex axially in the innermost dissepimentarium. *H. hexagona* has corallites that are much larger and have many more septa than does *H. oweni*; in addition, topotype colonies of *H. hexagona* all have heavily dilated septa and well-developed “carinae” locally.

H. oweni resembles *H. bassleri* of the Lime Creek Formation in these same characters, but has fewer septa, and in small corallites has shorter septa that are stouter in the outer dissepimentarium. *H. bassleri* also can become extremely large (as *H. bassleri magna*).

This species has a general resemblance to several *Hexagonaria* species from Frasnian strata of western Europe. Relationships and species boundaries have not yet been determined for this complex group.

Occurrence.—*H. oweni* is the typical Nora species of this genus. The types established by Belanski all came from the “*Prismatophyllum zonule*” of Belanski, at Rudd, Iowa, which he reported was the lower stromatoporoidal biostrome of the Nora (1927, p. 352). The specimens collected by me are exclusively from the basal meter of the upper Nora biostrome, with a few specimens coming from the McEachron Quarry, south of Portland (Locality 13, Appendix), and with approximately 30 specimens collected from the basal beds of the upper Nora biostrome at the locality south of Rockford, Iowa (Locality 21).

***Hexagonaria inequalis* (Hall and Whitfield, 1873)**

Platé 2, figure 5; Plate 34, figures 3–5; Plate 35, figures 1–5; Plate 36, figures 1–4

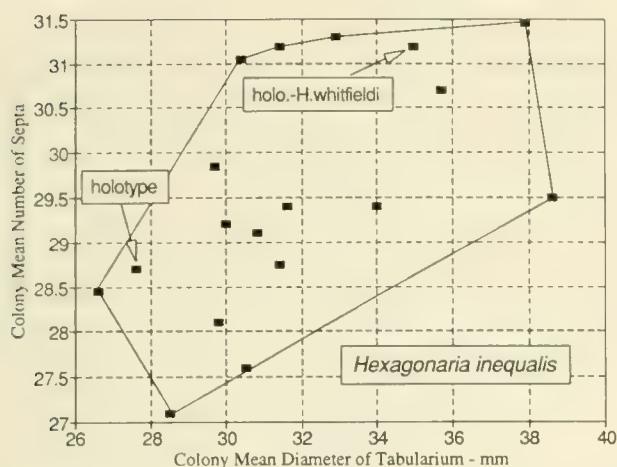
Acervularia inequalis Hall and Whitfield, 1873, p. 233, Pl. 9, figs. 11, 12; Clarke, 1903, p. 34; Fenton and Fenton, 1924, p. 56, Pl. 14, figs. 7.8.

Acervularia whitfieldi Fenton and Fenton, 1924, p. 57, Pl. 14, figs. 1–3.

Diagnosis.—Variable species of *Hexagonaria* with small corallites and marked septal dilation. Septa in two orders with major septa reaching to axis of corallites where they meet or join. Mean diameter of tabularia varying within a broad spectrum of from approximately 2.5 to nearly 4 mm, with small corallites having small diameters, narrow dissepimentaria and short, stout septa, sometimes with slightly zigzag wall between corallites. Colonies with larger corallites have larger diameter of tabularium, broader dissepimentaria and septa that are elongate and thin in the outer dissepimentarium, abutting against straight intercorallite walls. All colonies studied have similar appearance in longitudinal section, with tabulae in axial and periaxial rows.

Description.—*Hexagonaria inequalis* is a variable species of the genus, having two end morphotypes, the result of population variation, that are quite different in appearance, resulting in taxonomic confusion. Colonies are cerioid, and generally somewhat small and flattened. The holotype is a colony 13 cm in diameter with a maximum height of 4 cm. Others range to diameters of 20 to 25 cm and heights of 6 or 7 cm and are generally both the size and the shape of thick plates. The calices are characterized by an incised, tabularial pit 2.5 mm deep and a flat peripheral platform, occasionally with an everted area in the inner dissepimentarium.

Corallites are generally small, and in the 18 coralla studied, the colony mean diameter of tabularium varies from 3 to 4 mm, and the mean number of septa ranges from 27 to 32 for the same colonies (Text-fig. 41). All of those colonies with very small corallite diameters are characterized by few septa. Within this population are seen two gradational morphotypes, one with crowded corallites, narrow dissepimentaria, small tabularia and very stout, thick septa, and a second with less crowded, larger corallites, broader dissepimentaria, larger tabularia and septa that are thinner and more elongate in the outer dissepimentarium. The two are intergradational. The lectotype of *H. inequalis*, from Hackberry Grove (Locality 28, Appendix), is characteristic of the first morphology, and in fact, has the smallest mean tabularium diameter of all the specimens studied (2.5 mm). Corallites in this colony are closely packed, with septa that are short and very stout



Text-figure 41.—*Hexagonaria unequalis* from the "rusty bed" of the Cerro Gordo Member, colony mean diameter of tabularium (in mm) plotted versus the colony mean for total number of septa in each corallite. The small diameter holotype of *H. unequalis* is here indicated, as well as that of *Hexagonaria whitfieldi*, here regarded as a junior synonym.

in the outer dissepimentarium, but with major septa that extend to corallite axes and either join or leave an extremely small open axial space (Pl.34, fig.3). The thick septa are dilated somewhat and make an almost solid ring around the outer tabularium by addition of stereome coating of the inner flank of the dissepimentarium. Intercorallite walls either are straight where stout septa of neighboring individuals are opposed, or slightly wavy where septa are offset in neighboring corallites. In many corallites the major septa are dilated by up to 50% in the innermost dissepimentarium; equally thick minor septa are not dilated, but simply retain their thickness throughout the dissepimentarium and tabularium.

The second morphotype in this species is one with greater distance between corallite axes and broader dissepimentaria (Pl.34, fig.5). Colonies of this type have septa that are thinner in the outer dissepimentarium, and intercorallite walls are straight. Septa may have swollen trabeculae in the outer dissepimentarium giving a carinate appearance, and dissepiments are large and globose in this area. Where these thinner septa are at all thickened, there is a resulting broader base at the wall, so that a series of triangular bases is present, buttressing the walls. These also have marked dilation in the inner dissepimentarium, but more spindle-shaped dilation, as typical in many species of this genus. Dilation is typically two to three times septal thickness in the outer dissepimentarium. This dilation, along with stereome coating of dissepiments in the innermost dissepimentarium, tends to form a heavy ring around the tabularium.

All individuals within this species have a similar

appearance in longitudinal section, regardless of their appearance in transverse view. The tabularium has a characteristic axial row of flat-topped, cap-like tabulae and periaxial rows of sagging tabulae (Pl.36, figs.2,4). The term "characteristic" here refers to the common occurrence of this type of tabularium in many *Hexagonaria* species with long septa, including *H. hexagona*. The dissepimentarium is filled with four to eight rows of bulbous dissepiments that can be large in the outer part of the dissepimentarium and also can be slightly everted to reflect a slight reflexing of the calcinal platforms.

Septal structure is again typical for the genus, with well-defined monacanthine trabeculae making a relatively small angle with the intercorallite wall ($<30^\circ$ N) and bending inward to the inner dissepimentarium where the monacanth flex toward the horizontal. This flexing is very characteristic of the species, as is clearly shown by Plate 34, figure 4, and Plate 36, figure 2.

Type Specimens.—Lectotype, chosen by Clarke, (1903, p. 34), *H. unequalis* NYSM 3000/1. (Fenton and Fenton referred to several topotypes as "plesiotypes": FMNH 26048 and USNM 78635). *Acervularia whitfieldi* holotype is UMMP 5319, paratype FMNH 26055.

Discussion.—Recognition of the two forms described above resulted in a second species being introduced in 1924, *Acervularia whitfieldi* Fenton and Fenton (1924, p. 57), for the morphotype with less crowded corallites and thinner septa in the outer dissepimentarium. As shown on Text-figure 41, the holotype proposed by the Fentons has a colony mean tabularial diameter of close to 3.5 mm and a correspondingly large mean number of septa (31.2), but these colonies were not thin-sectioned by Fenton and Fenton, with resultant confusion. Their paratype is small and very similar to the lectotype of *H. unequalis*, with short, thick septa. The Clarke lectotype of Hall and Whitfield's species was not sectioned until the present study. The specimen of *Acervularia unequalis* figured in calicinal view by Fenton and Fenton (1924, pl.14), when sectioned, is a corallum with thin septa in the outer dissepimentarium (Pl.35, fig.2), indicating that these authors had difficulty separating their species from that of Hall and Whitfield. The two are regarded here as synonyms.

Variation between the two morphotypes in this population of *Hexagonaria unequalis* is seen in Text-figure 41, which shows colony means for septal number plotted versus tabularial diameters. Colonies with small corallites are characterized by thicker septa while forms with larger corallites are characterized by thinner septa. *Hexagonaria unequalis* in its thin-septaed morphotype is a very typical species of the genus and

resembles *H. hexagona*. It also resembles *H. bassleri* of the Owen Member in that both have long major septa that thin in the broad dissepimentarium. *H. inequalis* is characterized by smaller tabularial diameters, and those colonies with extremely small corallites and septa of uniform thickness are easily differentiated from any other species.

Occurrence.—*H. inequalis* was noted by Fenton and Fenton as occurring in the upper part of the Cerro Gordo Member, as does *H. whitfieldi*. More precisely, they noted both as occurring within the "*Stromatoporella* faunule" in the upper part of their "*Spirifer* zone" (1924, pp. 57, 58). Both of these morphotypes, regarded here as a single species, were collected only from a single bed recognized at two sections south of Portland, Iowa (Localities 27 and 27A, Appendix) and at the type section of the Lime Creek Formation (Locality 28), where the species is very abundant, but occurs only within a single 0.5 m-thick silty limestone bed (the "rusty-weathering" bed) that is characterized by abundant specimens of *Iowaphyllum*, *Pachyphyllum*, *Alveolites*, and stromatoporoids. It occurs approximately 8 m (26 ft.) below the basal beds of the Owen Member. The lectotype and Fenton topotypes of *H. inequalis* are both labeled as coming from Hackberry Grove (Locality 28 of this study). The holotype of *H. whitfieldi* was chosen from the Rominger Collection at the University of Michigan and is labeled as being from Cerro Gordo County, Iowa, while the paratype is simply labeled as from Rockford, Iowa. I would presume that the locality is the same as all other colonies collected (Hackberry Grove).

Family PHILLIPSASTREIDAE Roemer, 1883

A generic framework for the Family Phillipsastreidae was outlined by Hill (1981, p. F281): it is here modified with respect to both solitary and colonial corals of the family. It is incorrect to use the simple presence or absence of "horseshoe dissepiments" as a major criterion for inclusion of genera in this family, or for inclusion of species within one of its genera. Definition of the exact meaning of this term, which pertains to characteristic dissepiments of the phillipsastreids is not broadly agreed upon. That is, the exact shape, and uniformity of size and shape of horseshoe-shaped dissepiments occurring at the tabularium-dissepimentarium border is not clearly defined. Furthermore, the degree of distinctness of this row of dissepiments from other dissepiments is not clearly defined with regards to taxonomic importance. A universal character in genera of this family, however, is the presence of a symmetrical fan of coarse, individually discrete, monacanth or rhipidacanth septal trabeculae. The axis of this branching or fanning coincides with

the presence of a sleeve of horseshoe-shaped or other upbowed dissepiments that reflect the up-pocketing of polypal flesh to form elevated calicinal skeleton surrounding the tabularium. These specialized dissepiments, when uniformly developed in a highly arcuate form with their base less than or approaching their maximum width, do indeed resemble horseshoes, and are universally agreed to be "horseshoe dissepiments". They are commonly coated with skeletal stereome, and thus are distinguished from other dissepiments by their thickness as well as by their shape. However, this feature is more variable than the presence of divergent (fanning) septal trabeculae and specialists working on this group can more profitably focus on the septal trabeculae than on dissepiments, whether "horseshoes", or "specialized", or merely differing in their shape from other dissepiments.

Within the Phillipsastreidae, Hill (1981) recognized several groups of genera, although she avoided assigning genera to subfamilies. It still remains to define genera accurately and convincingly prior to subdivision of this complex. Hill (1981, p. F281) also presented the taxonomic history of the family and previously proposed subfamilies.

Genus PACHYPHYLLUM Milne-Edwards and Haime, 1851

- Phillipsastrea* d'Orbigny, 1849, p. 12 (in part); Smith, 1945, p. 36; Rozkowska, 1953, p. 57; Schouppé, 1958, p. 233; Strusz, 1965, p. 564; Sorauf, 1967, p. 22; Pickett, 1967, p. 25; Scrutton, 1968, p. 210; Coen-Aubert, 1973, p. 10; 1974, p. 9; Birenheide, 1978, p. 99; Hill, 1981, p. F281; Coen-Aubert, 1987, p. 46; McLean, 1989, p. 239; 1994a, p. 53.
- Pachyphyllum* Milne-Edwards and Haime, 1850, p. 68; 1851, p. 397; Rozkowska, 1953, p. 39; Schouppé, 1958, p. 233; Semenov-Tian-Chansky, 1961, p. 303; Birenheide, 1978, p. 115; Sorauf, 1978, p. 818; McLean, 1986, p. 444; 1989, p. 240; McLean and Sorauf, 1989 p. 392; McLean, 1994b, p. 78.
- Medusaephyllum* Roemer, 1855, p. 33; Scrutton, 1968, p. 210; Sorauf, 1988, p. 173; McLean and Sorauf, 1989, p. 392.
- Pseudoacervularia* Schlüter, 1881, p. 84; Rozkowska, 1953, p. 49; Pickett, 1967, p. 26.

Type Species.—*Pachyphyllum bouchardi* Milne-Edwards and Haime 1850, p. 68, from the Upper Devonian of Ferques, France. Neotype for this species (Muséum Nationale d'Histoire Naturelle in Paris, No. Z114a) here designated.

Diagnosis.—Variable genus of massive corals with thamnasteroid, astraeoid, or aphroid colonies. Species characterized by long septa dilated over specialized dissepiments appearing in longitudinal section as straight to somewhat irregular row of upbowed dissepiments which most commonly form uniform row of horseshoes. Horseshoe dissepiments are generally thickened by secondary layers of skeletal stereome. Septal trabeculae monacanth to rhipidacanth, in sym-

metrical fans with axis of fan located over sleeve of horseshoes. Commonly characterized by prominent calicinal necks protruding from external calicinal surface, with central depression at tabularium.

Discussion.—The specimens illustrated by Milne-Edwards and Haime (1851, pl.7, figs.7,7a,7b) have apparently been lost, and I here designate the topotype figured by Semenoff-Tian-Chansky (1961, p. 313, pl.9) as neotype.

The nomenclatorial aspects of the genus *Pachyphyllum* have been much discussed. After many attempts to find an acceptable way to differentiate species of this genus from those of *Phillipsastrea*, no consensus exists. Species of the two genera have much in common, and without doubt, are very closely related; in fact, they are considered synonyms by many coral workers.

In an early study of phillipsastreid corals, Smith (1945, p. 37) made a number of important observations, as follows: there is much variation in morphology within species then assigned to *Phillipsastrea* s.l.; horseshoe dissepiments are very well developed in many species, but not in all. Epitheca is generally absent, although traces of it are seen in some coralla. He regarded both *Medusaephyllum* and *Pachyphyllum* as synonyms of *Phillipsastrea*.

Rozkowska (1953) dealt extensively with colonial Givetian and Frasnian phillipsastreids, and placed species with well-developed septal dilation and horseshoe dissepiments in the genus *Pachyphyllum*, putting pseudoceroid species with horseshoe dissepiments in *Pseudoacervularia*. She placed species lacking clearly developed horseshoe dissepiments in *Phillipsastrea* (1953, p. 57). Schouppé illustrated the holotype of *Phillipsastrea hennahi* which indicates that it has horseshoe-like dissepiments in the inner dissepimentarium (1958, p. 233, pl.5, fig.1). He placed *Pachyphyllum*, *Medusaephyllum* and *Pseudoacervularia* into synonymy with *Phillipsastrea* as he defined it. He mistakenly utilized the name *Billingsastraea* for those corals of the family lacking horseshoe dissepiments (1958, p. 237) and illustrated *P. goldfussi* as an example (p. 236, fig.25).

Semenoff-Tian-Chansky described in detail a new species of *Pachyphyllum*, *P. chenouensis*, from Algeria (1961, p. 304) and included an extended description of a specimen of *P. bouchardi* in the same publication. This topotype of *Pachyphyllum bouchardi* is here designated neotype for the species. *Pachyphyllum bouchardi*, as well as the Algerian corals, has corallites that are large, with a diameter in the neighborhood of 10 mm (1 cm) or somewhat larger (up to 16 mm in the type species). Both species likewise have very

well-developed, stereome-thickened horseshoe dissepiments.

In a monograph on the Phillipsastraeidae, Scrutton (1968, pp. 210–212) reviewed both the family and the morphology of its prominent genera. He regarded *Pachyphyllum*, *Medusaephyllum*, and *Pseudoacervularia* as synonyms of *Phillipsastrea*, and placed pseudoceroid, astraeoid, thamnasteroid and aphroid corals in the genus, with or without the development of well-developed horseshoe dissepiments at the outer border of the tabularium. Scrutton (1968, p. 231) added to the nomenclature of the massive phillipsastreids by proposing the genus *Frechastraea* for pseudoceroid to astraeoid corals with fans of septal trabeculae but rare or absent horseshoe dissepiments. This is a clearly defined group of species that had previously been assigned to several different genera. Scrutton (1968, p. 212) additionally included cerioid colonies with horseshoe dissepiments in *Phillipsastrea*; it now appears better to put these in *Trapezophyllum* as redefined by Hill (1981, p. F284), and discussed below.

In the 1970's there were a number of definitions of colonial phillipsastreid genera, without developing consensus. Coen-Aubert (1973, p. 10) discovered an important specimen, a rare occurrence of *Pachyphyllum bouchardi* at the base of the upper Frasnian sequence of the Ardennes of Belgium, although she regarded it as *Phillipsastrea* (1973, p. 10). Birenheide (1978), in his treatise on corals of the Devonian of Germany, recognized *Phillipsastrea*, with the synonym *Pseudoacervularia*, as containing pseudoceroid, astraeoid and thamnasterioid colonies. He noted that *Phillipsastrea* bears distinct calicinal prominences surrounding the tabularium, but was of the opinion that there is no sleeve of true horseshoe dissepiments surrounding the tabularium in the holotype of *P. hennahi* (1978, p. 100), and suggested that none of the English phillipsastreids have uniform horseshoe dissepiments. Birenheide utilized two genera for those species with well-developed, thickened, uniform horseshoe dissepiments, the first being *Pachyphyllum* (1978, p. 116), for corals with large corallites and axially-inclined dissepiments interior to the sleeve of horseshoes. He also figured *P. bouchardi* from Bad Grund in the Harz Mountains of Germany. Additionally, Birenheide (1978, p. 116) retained the genus *Medusaephyllum* for colonial species with smaller diameter corallites and well-developed horseshoe dissepiments directly surrounding the tabularium.

In 1978, I suggested criteria for distinguishing species of *Pachyphyllum* from those of *Phillipsastraea* (1978, p. 819); namely, 1) presence of a uniform row of horseshoe-shaped dissepiments, 2) stereome coating on dilated septa and horseshoe dissepiments, 3) in

some species, a small axial structure formed by long major septa, 4) presence of some species with large corallite sizes and numerous septa, 5) tendency toward the development of aphroid colonies and a lack of pseudoceroid colonies, and 6) a tendency to develop flat-sided dilation of septa with discrete rhipidacanth septal trabeculae present, both in septa and extending over the tops of horseshoes. Species with these characteristics were placed in the genus *Pachyphyllum*, and it was emphasized that no single criterion or simple combination of several criteria could be used to categorize species of these two genera. It is possible, however, to recognize individual species (each of which is variable) and equally possible to place species in one genus or the other, even though uncertainties exist about proper placement of some.

Hill, in the revised *Treatise on Invertebrate Paleontology* volume on the Rugosa (1981) recognized *Phillipsastrea*, and placed into synonymy (with a query) the following genera: *Pachyphyllum*, *Medusaephyllum*, and *Pseudoacervularia*, thus taking a very conservative approach to the taxonomy of the group. She also recognized *Frechastraea* as a separate genus of phillipsastreids (p. F284).

In a series of developments in the 1980's, nomenclature shifted again. In a paper on species of phillipsastreids with large diameter corallites, McLean (1986, p. 445) restricted the use of the name *Pachyphyllum* to a genus name for species with well-developed horseshoes, etc., as suggested by Sorauf, but included as additional criteria, the tendency to form colonies with few corallites, and a form of budding in which the founder corallite is large and elongate, while buds are relatively few. McLean did not specifically note corallite size as a characteristic, but he only chose large diameter species for inclusion in the genus. This definition is not far from that of Birenheide (1978), but does not mention the presence of internal dissepiments. He did illustrate specimens with these characteristic dissepiments in mature corallites (1986, p. 451), and apparently this feature correlates with large corallite size, both here and in the solitary genus *Macgeea*. McLean (1986, p. 445) also here stated that *Medusaephyllum* was an appropriate name, as used by Birenheide for corals with characteristics similar to *Pachyphyllum* as he defined it, but lacking the "*bouchardi* growth form".

Several years later, I also utilized this genus name *Medusaephyllum* for species previously placed in *Pachyphyllum*, but with the exclusion of those with large diameter corallites, suggesting (1988, p. 173) that use of three generic names was appropriate for astreoid and thamnasterioid phillipsastreids, *Phillipsastrea*, *Pachyphyllum* and *Medusaephyllum*. The same approach

was used by McLean and Sorauf in their paper on the distribution of Frasnian corals in North America (1989, p. 392). Shortly thereafter, McLean (1989, p. 239) revised his definition of the three genera, using *Phillipsastrea* to cover all species with horseshoe dissepiments and variation ranging from colonies with weak and intermittent development, to those with "a continuous pipe completely surrounding the tabularium". He placed *Medusaephyllum* into synonymy with *Phillipsastrea*. He did, however, retain *Pachyphyllum* as the genus name for species with few, large corallites.

Utilizing corallite size alone is not a satisfactory means of separating species such as *P. bouchardi*, *P. chenoensis*, and *P. crassicosatum* from smaller but similar forms. In the Iowa fauna, the size range of *P. crassicosatum* overlaps with that of *Pachyphyllum woodmani*. *P. crassicosatum* does have rare small colonies that resemble budded individuals of *Macgeea*, and are characterized by an elongate protocorallite. This elongated, mature protocorallite can also occur in *Pachyphyllum woodmani* (Pl.2, figs.8–10), thus, the feature is seen in colonies of both large diameter corallites, and ones with smaller diameters. McLean (1989, p. 240; 1994a, p. 53) noted again that development of horseshoe dissepiments is a highly variable feature within some species that he assigned to *Phillipsastrea*, and did not consider the generic separation of this genus and *Medusaephyllum* as practical on the "basis of horseshoe dissepiment development". He did not comment on either the scheme of Sorauf (1978), or that of Birenheide (1978), which were *not* based on this single feature, which has often been judged as highly variable and not practical as the single basis for differentiation of species or genera. McLean (1994a, p. 70) also utilized the name *Chuanbeiphyllum* for totally aphroid phillipsastreids, such as *P. vesiculosa* from western Canada. No fully aphroid species are present in the Frasnian faunas of Iowa, thus I have nothing to add to the discussion. McLean (1994b, p. 78) has since reiterated his 1989 definition of *Pachyphyllum* based on colonies having a "distinctive growth form", with few, large corallites and the development of horseshoe dissepiments adjacent to the tabularium. I do not accept this restriction of the generic definition for two reasons, 1) the elongate nature of the founder corallite also occurring within some specimens of *Pachyphyllum woodmani*, and 2) the overlap in corallite size in *Pachyphyllum crassicosatum* and in *P. woodmani*. *Pachyphyllum crassicosatum* most commonly has a growth form with many large corallites, and other large diameter species assigned to this genus all are characterized by the pres-

ence of normal, sloping dissepiments internal to the horseshoe forms, as proposed by Birenheide (1978).

There are recognizable groups of species within the massive colonial phillipsastreids, and to ignore these is potentially to ignore the evolutionary development of these corals and also obscure the biostratigraphic value of them.

These groups can be summarized as follows:

1. There is a conservative group of corals which comprises species that do not show marked uniformity in their development of horseshoe dissepiments. Some species may show little differentiation of the inner dissepiments, but all have somewhat everted calices, all have fans of septal trabeculae, all have the tendency to have long septa that are dilated at the inner border of the dissepimentarium, and all have a pseudoceroid to thamnasterioid colonial form. All species are variable, thus it is an error to use one individual corallite or one colony as the basis for acceptance or rejection of species or genus assignment. This group of species is typified by *Phillipsastrea hennahi*, itself a highly variable species. Closely related species with pseudoceroid colonial form and little or no development of specialized dissepiments, but with fanning septal trabeculae, are placed in *Frechastrea*.

2. There is a group of species that are advanced in that they have a complete tube or sleeve of uniform horseshoe-shaped dissepiments and marked septal dilation. They generally lack internal dissepiments and do not have the pseudoceroid colonial form, rather, they may have an aphroid colonial form, and have calicinal prominences around the tabularium. This group of species also generally have relatively small diameter corallites, in the 3–8 mm range. This group of species is typified by *Pachyphyllum woodmani*.

3. There is another group of advanced species, fewer in number, but distinctive in appearance because of the presence of internal dissepiments inside the sleeve of horseshoe dissepiments and large corallite diameters (in the range of 10–16 mm). These species also tend towards the aphroid colonial form or may have confluent septa between corallites. The species *Pachyphyllum bouchardi* and *P. crassicostatum* have the general characteristics of this group.

Distribution.—*Pachyphyllum* has a wide geographic distribution, and is found in many of the major areas of outcrop of Upper Devonian (Frasnian) strata; Iowa, western United States and Alaska, western Canada, Germany, France, Russia, Poland, and China.

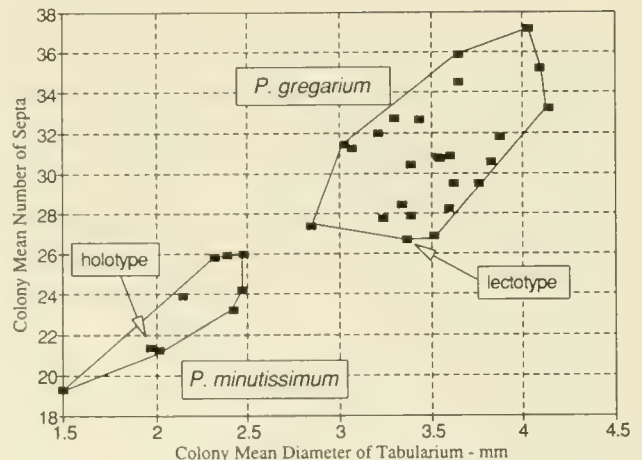
***Pachyphyllum minutissimum* Webster, 1905**

Plate 36, figure 5; Plate 37, figures 1–6; Plate 38, figures 1–6

Pachyphyllum minutissimum Webster 1905, p. 70.

Phillipsastrea exigua Lambe, Smith 1945, p. 41, Pl. 21, figs. 3–6;

McLean, 1994, p. 63, Pl. 5, figs. 3,4.



Text-figure 42.—*Pachyphyllum minutissimum* from the top of the Mason City Member, and *Pachyphyllum gregarium* from the upper biostrome of the Nora Member, colony mean diameter of tabularium (in mm) plotted versus the colony mean number of total septa. These are two of the abundant species of the genus found in the Shell Rock Formation. The holotypes of both are identified on the graph.

?*Phillipsastrea nevadensis* Stumm, 1940, p. 66, Pl. 7, fig. 13, Pl. 8, fig. 15; McLean, 1994, p. 62, Pl. 3, figs. 5–7, Pl. 4, figs. 1–6, Pl. 5, figs. 1,2,5–10, Pl. 6, figs. 1–4,7.

Diagnosis.—Thamnasterioid species of the genus with small corallite diameter and few septa. Septa typically fusiform, generally greatly dilated over horseshoe dissepiments to form solid ring around the tabularium. Two colony forms are present, one with very short major septa, another with septa reaching to the axis and joining. Septa generally confluent from corallite to corallite. Tabulae mostly complete and either flat or composite of flat to inclined or sagging incomplete tabulae that form a flat base to the calicinal depression.

Description.—Small compact colonies of this species have corallites with a small diameter tabularium, colony means varying from 1.5 mm to 2.8 mm., and colony mean septal numbers from 19.3 to 27.5 in 19 specimens (Text-fig. 42). In the type specimen and numerous other colonies assigned to this species, major septa are short, leaving a septa-free axial area that is from $\frac{1}{3}$ to $\frac{2}{3}$ the diameter of the tabularium (Pl.36, fig.5). In its most extreme form, this type of colony has corallites in which the major septa extend only slightly into the tabularium. The septa are all dilated, and are spindle-shaped, with maximal dilation in the area of the horseshoe dissepiments, where septa join laterally in a few specimens, but with dilated septa ending as a blunt termination in the tabularium. The major septa are characteristically fat and spindle-shaped in cross-section (Pl. 37, fig.1). In one group of colonies assigned to this species, generally those with larger diameters than the holotype, major septa are

long and extend to the axis of the corallite, where they join (Pl.37, figs.3–5). Where long major septa join at the corallite axis there is no swirling of septa around the axis, rather the septa join in a somewhat pinnate arrangement suggesting order of insertion in the calice, with the first-formed joined across the corallite axis. Septa may be quite heavy in the outer dissepimentarium, and generally are about $\frac{1}{2}$ their dilated width. Septa in these corallites are confluent with or abutting those of neighboring corallites, except where budding produced young aphroid individuals.

The ring of horseshoe dissepiments seen in transverse sections is generally heavily coated with stereome in *P. minutissimum*, with a solid ring of dilated septa and stereome-coated horseshoes surrounding the tabularium (Pl.38, fig.1). Minor septa do not extend past this ring into the tabularium, and in extreme cases the major septa only just do extend beyond it.

The tabularium, seen in longitudinal section, has flattish to slightly arched or sloping, complete to incomplete tabulae (Pl.37, fig.2). There are no axial or periaxial rows of tabulae. The completeness of the tabulae varies with the size of the tabularium and length of major septa. The smaller the tabularium, and the shorter the major septa, the greater the tendency for tabulae to be complete.

The dissepimentarium is marked by uniform horseshoe dissepiments forming a wall surrounding the tabularium (Pl.38, figs.4,6). There are no dissepiments inside the horseshoes. The horseshoes are coated with stereome, and in some specimens the coating is as thick as the dissepiments are wide, so that the coating extends over the whole horseshoe rather than only being a coating on the inner and outer flanks of the row. The outer dissepimentarium is characterized by large and irregular dissepiments. In those colonies with the smallest tabularia the outer dissepiments may be almost as large as the tabulae.

Trabecular fans are very tight in this species, and rhipidacanth trabeculae are of small diameter and are packed closely together (Pl.38, fig.4). The lateral divergence of rhipidacanth trabeculae is clearly seen in transverse sections of greatly dilated septa. The fans are centered on the horseshoe dissepiments, and trabeculae in the outer dissepimentarium are nearly vertical (Pl.38, fig.6).

Type Specimen.—Holotype USNM 78648.

Discussion.—Text-figure 42 illustrates the mean diameters of the tabularium in nine colonies of *P. minutissimum*, and shows the wide range in size for this species. The collection of colonies from the Nora Dam locality are all towards the large end of the scale, while the two smallest individuals are from the southern part of the geographic range, from Rosedale and from Mar-

ble Rock. The Marble Rock corallum has the smallest tabularial diameters (and least variation between them). Study of small-diameter corallites in this colony and others (including the holotype) shows that these smallest corallites likewise have 1) short major septa, 2) the most complete tabulae, 3) the most solid peritabular sleeve of dilated septa and stereome, and 4) the greatest confluency of septa between corallites (Pl.36, fig.5; Pl.37, fig.1). Colonies with larger-diameter corallites are most likely to have longer septa which join at the corallite axis (Pl.37, fig.5). Likewise, in these larger forms, dilated septa generally do not form a solid ring at the position of the horseshoes.

Budding appears to affect corallite morphology in several ways. Young corallites are commonly aphroid, and gradually become more nearly confluent as they mature, and septal dilation is less developed in immature forms, becoming more marked with maturity.

One colony of *P. minutissimum*, collected from the Nora Dam population has a very weakly calcified skeleton, with little or no septal dilation. There is a slight amount of stereome on the horseshoe dissepiments, but none elsewhere. The dissepiments in the outer dissepimentarium are very large and irregular, the horseshoe dissepiments are irregular, and there are many fewer complete tabulae than normal for this species. I regard this as pathological.

There is uncertainty regarding possible conspecificity of *P. minutissimum* and *P. nevadensis* (Stumm, 1940). In the specimen figured by Stumm (1940, p. 64), septa are long, extending almost to the axis. Stumm noted that the diameter of the tabularium averages 3 mm (p. 66), which is too large for *P. minutissimum*, except for occasional colonies within the Iowa population. The specimen figured by McLean and Sorauf from western Canada (1989, pl.1, figs.8,9) has tabularial diameters in the range of 2.5 mm and mean number of septa that is close to 24. The dilation is not particularly marked in this individual, but septal confluency is well developed. The major septa in many of the corallites in this Canadian corallum do not extend into the tabularium. As interpreted by McLean (1994, p. 62), however, *P. nevadensis* is a highly variable species, with diameter of tabularium, number and length of septa, and in colonial form varying enough to encompass the Iowa specimens of *P. minutissimum*, which however, would have priority over the Stumm species from Nevada. *Phillipsastrea exigua*, from Frasnian strata of the Hay River region of western Canada, has been placed into synonymy with *P. nevadensis* by McLean, who also figured its holotype (1994, p. 63, Pl.5, figs.3,4). *P. exigua* closely resembles many specimens of *P. minutissimum*, and is placed therein.

Pachyphyllum minutissimum resembles several species from Frasnian units of New Mexico. *Pachyphyllum variabile*, from the Sly Gap Formation is somewhat smaller in mean diameter than is *P. minutissimum*, but primarily differs from the Iowa species by its tendency for septa to break up into trabecular pillars in the dissepimentarium. *P. confluens*, from the late Frasnian Contadero Formation, is approximately the same size and has approximately the same number of septa as does *P. minutissimum*, but is marked by greater confluency of septa between corallites and reduced dilation of septa. This New Mexico species was represented by a single specimen found in the uppermost Frasnian bed of the Contadero, thus is difficult to evaluate. It may belong in the Iowa species.

Occurrence.—*P. minutissimum* is the most common species of the genus in the uppermost unit of the Mason City Member. The holotype collected by Webster is labeled as originating from the Shellrock Formation at Nora Springs, Iowa; by its matrix composition and the common occurrence of the species, it presumably came from the uppermost meter of the Mason City Member in Nora Springs. The species has also been collected from the top of the Mason City at Koch's reference section on the south side of Nora Springs (Locality 11, Appendix), from the upper 0.5 m of the Mason City at its type section (Locality 9) and from this horizon at the dam at the north edge of Nora Springs (Locality 8). It also occurs in the same position at the top of the Mason City at Cooper's Bend (Locality 19), Roseboro (Locality 22), and from the most southerly outcrop examined, the Maxson Quarry at Marble Rock (Locality 23). The range of this species is consistent within the study area.

***Pachyphyllum gregarium* Webster, 1905**

Plate 1, figure 8; Plate 39, figures 1–5; Plate 40, figures 1–5

Pachyphyllum woodmani var. *gregarium* Webster, 1905, p. 70.

Diagnosis.—Variable species with tabularial diameter in the mid-range for North American species of the genus (3–4 mm) and number of septa ranging from 26 to 35. Septa usually short, leaving approximately $\frac{1}{3}$ of the tabularium open at the axis. In some colonies, septa even shorter, with major septa only penetrating a short distance into tabularium. Septa dilated to varying degrees, but usually occupy at least 50% of the area of the horseshoe dissepiments, and may be dilated sufficiently to form a solid ring around the tabularium. Septal confluency variable, but most commonly, septa are confluent with or abut against those of neighboring corallites. Tabularium occupied only by complete, flat or sloping tabulae.

Description.—*P. gregarium* forms small, compact colonies. Four such colonies were available from the Rudd section, including the lectotype and paralectotype collected by Webster, as well as two topotypes collected by me. The Rudd fauna has colonies that vary only from 3.4 to 3.6 mm in colony mean diameter of tabularium, and from 26.8 to 28.2 for mean number of septa.

A larger sample of colonies from south of Rockford (Locality 21, Appendix) and Tom Williams Quarry (Locality 16) shows much more variability, from 3.2 to 4.3 mm in colony mean tabularium diameter, and from 27.8 to 37.2 in mean number of septa for 18 colonies (Text-fig. 42). There appears to be one cluster for Rudd colonies and another, larger cluster by size and septal number, of colonies from west and south of Rudd.

In its most typical development, *P. gregarium* is composed of corallites mostly of the same approximate size, with septa either confluent with or abutting against septa of neighboring corallites. Where much budding has occurred, with a correspondingly large number of juveniles, many corallites are aphroid, and in several colonies, the aphroid form is pervasive in portions where budding has been abundant (Pl.39, figs.1,4).

Septa are clearly differentiated into major and minor, and minor septa do not extend inside the sleeve of horseshoe dissepiments. Major septa generally extend $\frac{1}{2}$ to $\frac{2}{3}$ of the way to the corallite axis, leaving a broad open area at the axis (Pl.40, figs.1,3). In several colonies, major septa are even shorter, only extending $\frac{1}{3}$ way into the tabularium (Pl.40, figs.2,4). Dilation is marked, but is often flat-sided, giving an elongate fusiform appearance to septa in transverse section. Septal dilation is one of the highly variable features of the species, in some corallites sufficient to fuse septa into a solid ring over the horseshoes, in others only forming a porous ring in transverse section, with septa occupying $\frac{1}{3}$ to $\frac{1}{2}$ the area at the ring of horseshoe dissepiments (as seen in transverse section). Also, in transverse section, stereome coating the outside of the horseshoe dissepiments is thick and can form a heavy envelope that coats both septa and horseshoes, reinforcing their wall-like appearance. Several colonies have very heavy dilation of septa accompanied by stereome in the area of the horseshoes (Pl.40, fig.3). These colonies tend also to have thick, heavy septa in the dissepimentarium and confluent septa with neighboring corallites with thick septa, suggesting a parent-offspring relationship.

In longitudinal view, several important characters of the species are seen. The horseshoe dissepiments are uniformly sized and swollen, and their inner flank is

often coated with stereome, as is the outer side of the sleeve. This coating is very thick in colonies with heavy skeletal development and heavy dilation of septa. No accessory dissepiments are seen between the horseshoes and the tabularium (Pl.40, fig.5). The tabularium is occupied by rather flat tabulae, most of which are complete and horizontal or gently sloping. In some colonies tabulae sometimes sag, and in others, accessory incomplete tabulae are occasionally present, leaning against the outer border of the tabularium, sloping in towards the tabularial floor (Pl.39, fig.5).

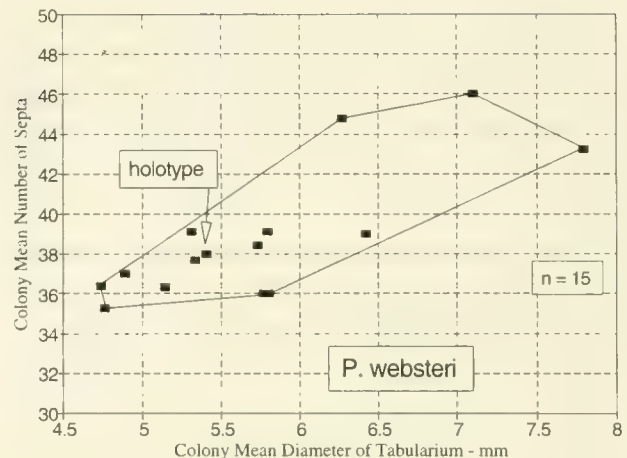
The outer dissepimentarium most commonly contains large, irregular-shaped to flat and elongate dissepiments, and extends into that of neighboring corallites, without a well-defined boundary. This is especially so in aphroid parts of a colony (Pl.40, fig.4).

Septal trabeculae form tight fans centered over horseshoes. Trabeculae in this species are closely packed into the fans, although rhipidacanth do not show the common separation and wide spacing of horizontal rhipidacanth trabeculae (such as seen typically in *P. crassicostatum*).

Type Specimens.—Lectotype USNM 78645B, designated here, paralectotype USNM 78645A (labeled cotypes by Webster).

Discussion.—This is the common species that occurs in biostromal carbonates of the Nora Member of the Shell Rock Formation. *Pachyphyllum gregarium* is characterized by rather large tabularial diameters and variation in the amount of confluency of septa between corallites. The lectotype specimens (USNM 78645A, 78645B) show considerable disruption of confluency, but the species as a whole shows great variability of this character. In its somewhat aphroid nature, the species resembles *Phillipsastrea disrupta* McLean, from western Canada. *P. disrupta* however, is larger and has more septa than *P. gregarium*, but is not far above the range seen in the Iowa species. *P. gregarium* shows a whole range from colonies with confluent septa (Pl.40, figs.1–3) to colonies with partially or wholly aphroid nature (Pl.39, figs.1,4, Pl.40, fig.4). Aphroid individuals are generally not greatly dilated, perhaps as a result of a relationship between the colony form and active budding. *P. gregarium* may be related to *P. disrupta*, but the two are not conspecific.

Occurrence.—*P. gregarium* is the common species of the Nora Member. Webster's types were collected from outcrops and a quarry on Flood Creek at Rudd, Iowa (Webster, 1905, p. 70), and topotypic material was collected here by me from the upper biostrome of the Nora Member (Locality 12, Text-fig. 15). Collection of a large number of colonies in an area bulldozed in 1967 during construction of the Shell Rock River bridge, 5.6 km (3.5 mi) south of Rockford, allows rec-



Text-figure 43.—*Pachyphyllum websteri* from the lower, biostromal beds of the Mason City Member, colony mean diameter of tabularium (in mm) plotted versus the colony mean number for the total septa in each corallite. The holotype of the species is identified on the graph.

ognition of a range of variation within this species, as discussed above. Individuals assigned to this species have also been collected from the lower biostrome of the Nora at Rockford (Locality 20, Appendix), from the basal few centimeters of the Nora outcrop (presumably the upper biostrome) at the County Roads Quarry (Locality 14), at Tom Williams Quarry (Locality 16), and far to the north at the quarry north of Keidle's Bluff, where it occurs in the basal centimeters of the upper biostrome of the Nora Member (Locality 1).

***Pachyphyllum websteri* Belanski, 1928**
Plate 41, figures 1–4; Plate 42, figures 1–5

Pachyphyllum websteri Belanski, 1928, p. 171, Pl. 12, fig. 3.

Diagnosis.—Species of the genus with large diameter tabularium and weakly aphroid colony form; with fusiform, dilated major septa that extend a variable distance into the tabularium. Stereome on horseshoe dissepiments is commonly sufficient to form a solid ring around the tabularium. Tabularium filled with complete, flat or inclined tabulae, but with inner dissepiments lining the tabularium, within the sleeve of horseshoe dissepiments.

Description.—*P. websteri* occurs as small colonies that are crowded with partially aphroid corallites. Colony mean tabularium diameter varies from 4.6 mm to 7.3 mm for 15 colonies studied, and the same colonies have mean septal numbers of from 35 to 45 (Text-fig. 43). The diameter of corallites is partly a function of maturity of the corallites (and their frequency of budding), and this group of colonies has a diameter for

the largest corallite that ranges from 5.4 to 9 mm, with a mean 6.7 mm for the population.

Septa are differentiated into major and minor septa on the basis of length and amount of dilation, with major septa commonly extending within the tabularium from $\frac{1}{3}$ to $\frac{1}{2}$ the distance to the corallite axis. Septal dilation is always well-developed, but because of the large diameter of the tabularium, septa still only occupy about $\frac{1}{2}$ of the space over the sleeve of horseshoe dissepiments (Pl.41, figs.2,4). Only in two colonies was sufficient stereome deposited over the horseshoe dissepiments to form a complete, solid ring around the tabularium. Dilation of major septa is also somewhat peculiar in this species, as much of the dilation of major septa occurs within the tabularium itself, and the belt of maximum dilation can be centered over an obvious band of stereome that coats the inner flank of the horseshoe dissepiments. Minor septa seldom extend farther toward the corallite axis than the inner margin of the horseshoes.

Horseshoe dissepiments are uniform and stacked in a straight sleeve surrounding the tabularium, but inner dissepiments occur within this sleeve, and are commonly seen in transverse section as asymmetrical curved dissepiments attached at one end to a major septum. Commonly three or four rows can be seen in transverse sections. Horseshoe dissepiments themselves are heavily coated with stereome both on their inner (tabularial) and outer sides. This coating can be as thick as the horseshoes are wide.

In longitudinal section, the tabularium is filled with tabulae that are often complete and sagging or inclined so that the calicinal pit is flat on the bottom, but sloping at the margins of the tabularium (Pl.41, figs.2,3). One to five rows of elongate, steeply inclined to vertical dissepiments are present axial to the horseshoe dissepiments (Pl.42, fig.3). The external dissepimentarium is filled with large, flattened, somewhat irregular dissepiments (Pl.41, figs.2,3). This outer dissepimentarium is rather narrow for the genus, and reflects the calicinal topography, with a depression between corallites expressed by rows of large and irregular dissepiments which are interspersed with rows of small, irregular ones. This size variation in dissepiments seems related to frequency of budding rather than periodic (seasonal?) variation in corallite diameter (Pl.42, fig.4).

The septal monacanthos of this species form tight fans centered on the horseshoe dissepiments (Pl.42, fig.3).

Type Specimens.—Holotype SUI 2176, paratypes SUI 529, USNM 71030.

Discussion.—Aphroid colonies of *P. websteri* are variable in their development (Pl.41, fig.2; Pl.42,

fig.4). In several, there is a suggestion of vertical banding of more aphroid and less aphroid portions of the colonies. In others, the axial portion of the colony is characterized by a higher percentage of recently budded corallites, and an accompanying more aphroid relationship between corallites. The apparent relationship between budding rate and the degree to which the aphroid colonial form is developed is striking; in numerous colonies budding is much more abundant in the axial portion of the colony, and indeed, corallites are more aphroid here. Where banding is suggested, this can be as easily related to seasonal variation in the rate of budding as to variation in rate of skeletogenesis. In one colony of *P. websteri*, twinned, axial budding occurred, originating directly from the tabularium of the parent (Pl.42, fig.5). This is the only example known to me of parricidal budding in the genus.

In its partially aphroid colonial form *P. websteri* is reminiscent of *Phillipsastrea disrupta* from western Canada (McLean, 1994, p. 67), but the Iowa species has larger tabularial diameters (up to 9 mm) and many more septa than *P. disrupta*. Another similar species is that described as *Pachyphyllum ibergense* var. *progressa* by Rozkowska (1953, p. 48, pl.5, fig.8). The Polish form is approximately the same size as *P. websteri*, but has many fewer septa and is more aphroid than the latter.

Occurrence.—The Belanski types are from lower Mason City biostromal beds in a former quarry in southern Nora Springs (Locality 11, Appendix). According to Belanski (1928, p. 174), *P. websteri* typically occurs in the lower biostromal beds of the Mason City, which he called the "*Aulopora* zone". Individuals of *P. websteri* have been collected in numbers from the lower Mason City biostrome at its type section (Locality 9, Appendix), south of Nora Springs (Locality 11), at Kapka's Farm (Locality 18), and at Cooper's Bend (Locality 19). In addition, three colonies with larger corallites have been collected from the lower biostrome of the Nora north of Nora Springs (Locality 2), at Reed Creek (Locality 4), and at Rudd (Locality 12). These few colonies fit well into *P. websteri*, having major septa dilated well into the tabularium, and with steeply inclined dissepiments occurring in the innermost dissepimentarium, inside the horseshoe dissepiments. In one of these colonies, skeleton is thicker than normal and septa tend to be confluent; more so than in some colonies of *P. websteri*. The Nora Member is generally characterized by *P. gregarium*, but the three specimens fit well into *P. websteri*, and I regard them as an upward extension of its local range (Pl.42, fig.6).

***Pachyphyllum woodmani* (White, 1870)**

Plate 2, figures 8–11; Plate 3, figures 1–4; Plate 43, figures 1–6; Plate 44, figures 1–5; Plate 45, figures 1–5; Plate 46, figures 1–6; Plate 47, figures 1–5

Smithia woodmani White, 1870, p. 188.

Pachyphyllum woodmani Hall and Whittfield, 1873, p. 231; Webster, 1889a, p. 622; Fenton and Fenton, 1924, p. 46, Pl. 7, figs. 1–3, Pl. 8, fig. 2, Pl. 9, figs. 11–12, Pl. 10, figs. 3; Ehlers, 1949, p. 2, Pl. 3, figs. 1–4; Stumm, 1949, p. 74, Pl. 17, fig. 24; Sorauf, 1978, p. 820, Pl. 1, figs. 1–4, Pl. 2, figs. 1–4, Pl. 3, figs. 1–5, Pl. 4, fig. 1.

Pachyphyllum ordinatum Webster, 1889a, p. 624.

Pachyphyllum levatum Webster and Fenton, in Fenton and Fenton, 1924, p. 48, Pl. 5, fig. 4, Pl. 12, figs. 9–10.

Pachyphyllum irregulare Webster and Fenton, in Fenton and Fenton, 1924, p. 49,

Pl. 10, figs. 1,2, Pl. 11, figs. 1,2.

Pachyphyllum crassicosatum nanum Fenton and Fenton, 1924, p. 52, Pl. 9, fig. 6.

Phillipsastrea woodmani Stumm, 1940, p. 64; McLean, 1994a, p. 58, Pl. 1, figs. 3–6, Pl. 2, figs. 1–6, Pl. 3, figs. 1–4.

Pachyphyllum vagabundum Ehlers, 1949, p. 1, Pl. 2, figs. 1–3.

Medusaephyllum woodmani Sorauf, 1988, p.175, figs. 20.3–20.6, 22.1–22.4, McLean and Sorauf, 1989, p. 393, Pl.1, figs. 3,4.

?*Phillipsastrea irregularis* McLean 1994a, p. 64, Pl. 6, figs. 6–8, Pl. 7, figs. 1–7, Pl. 8, figs. 1–3,5.

Diagnosis.—*P. woodmani* consists of small to medium-sized coralla with markedly exsert corallites. Septa dilated at boundary between tabularium and dissepimentarium, forming sleeve around tabularium. Uniform sleeve of horseshoe dissepiments most commonly, but not invariably, formed under area of septal dilation. Septa most often confluent between corallites, but colonies sometimes partially aphroid. Major septa long and either reach to axis and unite to form aulos-like structure, or reach near axis and swirl around small open space. Minor septa generally extend only short distance past the horseshoe sleeve into tabularium. Dissepimentarium characterized by interior, steeply inclined dissepiments inside heavily stereome-coated horseshoe dissepiments. Outer dissepiments normal with varying sizes, merging with outer parts of neighboring corallites.

Description.—*P. woodmani* generally occurs in flattened colonies with sharply exsert corallites. Corallites are of medium diameter for the genus, and colonial form generally is thamnasterioid, more rarely partially aphroid (Pl.43, figs.1–3). The species is characterized by well-developed, uniform horseshoe dissepiments. This, together with pronounced septal dilation, forms a solid sleeve around the tabularium, made of divergent rhipidacanth trabeculae plus abundant stereome coating the horseshoes. The outer dissepimentarium is formed of numerous globose dissepiments, with layers of larger, irregular dissepiments occurring at regular intervals. Major septa are long and commonly deflected in the axial area to form a structure approaching,

but not attaining the solid ring of an aulos (Pl.43, figs.4,5,6). Minor septa most commonly do not extend beyond the thickened collar zone of the inner dissepimentarium. There are one to four rows of steeply inclined dissepiments, inside the ring of horseshoe dissepiments. The tabularium has flat to slightly sagging tabulae peripherally, and axial disruption of tabulae by long septa, so that in some corallites there is the development of an axial row of tabulae.

Type Specimens.—Neotype NYSM 3580/1, designated by Sorauf (1978, p. 821). Topotypes of *P. woodmani*, FMNH 26016, 26017, were noted as “plesiotypes” by Fenton and Fenton (1924, p. 47). Species synonymized with *P. woodmani* are; *Pachyphyllum ordinatum*, holotype, USNM 78646, *P. levatum*, holotype USNM 78629, *P. irregulare*, holotype USNM 78615, and the subspecies, *P. crassicosatum nanum*, holotype FMNH 26018.

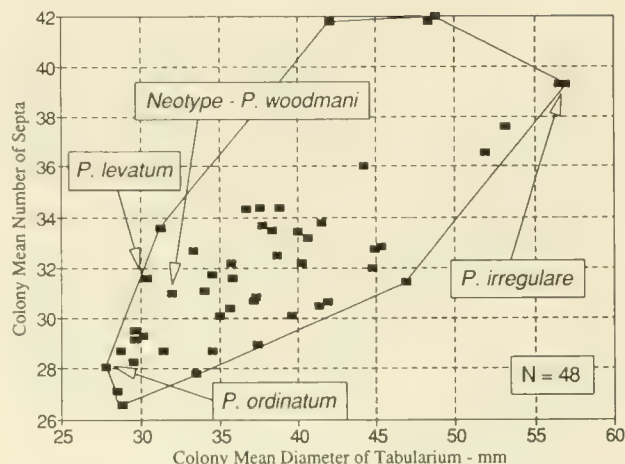
Discussion.—The highly variable species *Pachyphyllum woodmani* is very abundant in the Cerro Gordo Member, especially in the upper part. At the time of the Webster and Fenton study, variability within this population was not well understood; thus species and subspecies names for variants of the species were proposed, generally on the basis of one or two colonies, at times without sectioning specimens.

The Hall and Whitfield neotype (NSYM 3580/1) is a good one, with characteristics that are very typical of the species (Pl.43, fig.4). This specimen has been thin sectioned and photos of sections published previously by Sorauf (1978, p. 821). The figured topotype of Fenton and Fenton, USNM 26017, also strongly resembles the neotype, although not having as much stereome thickening on horseshoe dissepiments. Septal dilation is not extreme in the neotype or in most topotypes, where about ½ of the perimeter of the tabularium is occupied by inflated septa. Dilation of septa has a “straight-sided” appearance, and is accompanied by the deposition of stereome on horseshoe dissepiments to form a marked “halo” around the tabularium. Of the two FMNH topotype specimens, one (26016) has septal dilation similar to that of the neotype, but heavier stereome coating; the other has similar dilation, but heavy stereome only present on the inner side of the horseshoes. Colony form varies somewhat, mostly in the amount of confluency of septa from one corallite to another. In most specimens, confluency is best developed where budding is not frequent, and is absent where budding occurs in the outer dissepimentarium.

Thin sections of the holotype of *Pachyphyllum ordinatum* Webster (1889a, p. 624) indicate that it belongs to a group common within *P. woodmani* characterized by diameters at the small end of variation

and very heavy dilation of septa accompanied by heavy deposits of stereome on horseshoe dissepiments (USNM 78646, Pl.45, fig.1). The occurrence of such colonies with very heavy collar of stereome surrounding the tabularium was recognized by Fenton and Fenton, who changed the status of the taxon to a subspecies, *P. woodmani ordinatum* (1924, p. 47). Because this occurs commonly within the *P. woodmani* population, I would not differentiate it from others. The morphotype is a distinct one, because of the solid collar surrounding the tabularium, with long major septa that are irregularly bent at the corallite axis, but do not swirl to form the small "pseudo-aulos" that is common within the species. Trabecular fans are also very tight, and trabeculae and stereome together can hide horseshoe dissepiments in longitudinal section. Fifteen corallites in the holotype have a mean tabularium diameter of 2.8 mm, with a colony mean number of septa of 28.1 (Text-fig.44). Thus, *P. ordinatum* comprises a group of *P. woodmani* with small-diameters, and the small corallites have few septa. Size is not uniform throughout all heavily dilated colonies within the species. Fenton and Fenton were correct when they wrote that, "there is in no respect a clear demarcation from the less exsert forms of *woodmani*" (1924, p. 48). As can be seen in Plate 46, figures 1–6, there is a complete spectrum from colonies with a relatively light weight skeleton to those with heavy calcification and abundant stereome, encompassing various "subspecies" of *P. woodmani*.

The holotype of the species *P. levatum* was not sectioned by Webster and Fenton. They illustrated photos of the external surface of these corals with prominent calicinal necks on the upper surface (Fenton and Fenton, 1924, pl. 12, fig. 9) and undersurfaces showing holotheca absent (eroded?), revealing prominent rounded corallites at the margins of colonies (Fenton and Fenton, 1924, pl. 12, fig. 10, and pl. 5, fig. 4). The latter is a photograph of the undersurface of a colony that obviously was turned over and lay exposed on the sea floor long enough for a sizeable colony of aulopodid corals to grow on it. Thin sections of the holotype show medium-sized corallites (mean tabularium diameter of 3.04 mm with mean number of septa of 31.6 for 16 corallites, Text-fig. 44). As can be seen in figures 2 and 3 of Plate 44, the holotype of *P. levatum* is clearly a specimen of *P. woodmani* with heavy septal dilation, moreso than in the neotype, but lacking the solid ring shown in transverse sections of the holotype of *P. ordinatum*. Septal dilation here is flat-sided and forms an almost solid collar around the tabularium. The tabularium is filled with flat, interrupted tabulae and is strongly reminiscent of the *ordinatum* holotype and also the figured specimens of Fenton and



Text-figure 44.—*Pachyphyllum woodmani* from throughout the upper units of the Cerro Gordo Member, colony mean diameter of tabularium (in mm) plotted versus the colony mean number for the total number of septa in corallites. The holotypes of synonymized species are also indicated on the graph, namely for *Pachyphyllum levatum*, *Pachyphyllum ordinatum*, and *Pachyphyllum irregulare*, all species of Webster or Webster and Fenton.

Fenton (FMNH 26016, 26017). Septa are confluent to a greater degree than in many colonies, but there also is an absence of budding in this section and the degree of confluency may thus reflect the growth stage within the colony.

Likewise the holotype and paratype of *P. irregulare* Webster and Fenton, in Fenton and Fenton, 1924, p. 49 were figured in external view only (1924, pl.10, figs.1,2). These are decorticated specimens with growth that is irregular in direction, and colonies feature very strongly exsert calicinal prominences surrounding tabularia. The holotype has ovoid corallites, and measuring the long diameter provides an exaggerated idea of their size. The longitudinal section is that of a very typical *P. woodmani*, except that it is a large *P. woodmani*. Five corallites in the holotype have a mean long diameter of 4.2 mm and a mean number of septa of 41.8 (Text-fig. 44), while a sixth corallite is incomplete, but apparently had a long diameter of 5.2 mm, large for a *P. woodmani* (Pl.47, figs.1,3). The paratype has even larger corallites; three corallites here have means of 5.7 mm for the long diameter and 39 for septa. In all other characters the types resemble *P. woodmani*. McLean (1994a, p.64) accepted this as a valid species, and included large numbers of *P. woodmani*-like corals from western Canada in his *Phillipsastrea irregularis*. Iowa specimens, however, fit within the size range of *P. woodmani*, and can not be differentiated from them.

The last of the taxa resulting from the Fenton and Fenton study is *Pachyphyllum crassicostatum nanum*

(1924, p. 52), which they reported as coming from the upper Cerro Gordo Member. No individuals have been seen in upper Cerro Gordo beds that warrant placement in this subspecies, and the one specimen figured by them in 1924, the holotype (pl.9, fig.6, FMNH 26018), strongly resembles *P. woodmani* in thin section, but with larger corallites than usual for the latter. Its only peculiarity is that it appears to have more strongly differentiated septal rhipidacanth than common in *P. woodmani*. Fenton and Fenton noted that the subspecies was uncommon, but was found at Hackberry Grove and at Rockford. No specimens were collected that resemble theirs.

Some small colonies show a long founder corallite that grew to adult diameter prior to budding (Pl.2, figs.8–10). As most of these founder corallites developed from larval settlement on a hard substrate, they sometimes have an impression of a brachiopod or other organic debris on their base (Pl.2, fig.10).

Occurrence.—Fenton and Fenton noted that *P. woodmani* is characteristic of the upper part of the Devonian of Iowa. They noted that it appears in the lower “*Spirifer* zone” and is present throughout the Cerro Gordo Member. They stated that, “In the Owen it is more or less replaced by varietal forms” (1924, p. 47). I did not find corals assignable to this species above the Cerro Gordo Member. Abundant specimens of *P. woodmani* were collected at all sizeable outcrops of the upper part of the member, the “*Spirifer* zone”. The neotype for the species comes from the former Rockford Brick and Tile Co. quarry (Locality 35, Appendix), where specimens were collected from all units of the argillaceous limestones and calcareous shales of the upper Cerro Gordo, which were stripped from underlying beds in order to quarry the shales of the Juniper Hill Member. Abundant *P. woodmani* were also collected from throughout the South Portland sections (Localities 27 and 27A) and especially from the “rusty bed”, at the type Lime Creek section (Locality 28), where the species is also abundant throughout the upper part of the sequence. Bird Hill and Bird Hill South (Localities 31 and 32) furnished many specimens also, as did County Road North (Locality 29). In all of these localities, the species was at one time extremely abundant. It is still abundant locally, but many localities have been heavily collected and specimens are less common. Colonies of *P. woodmani* are most easily found in numbers today by searching in plowed fields (Locality 28b) neighboring the type Lime Creek section.

The species also occurs in western Canada, New Mexico, Nevada and New York.

***Pachyphyllum crassicosatum* Webster, 1889**

Plate 3, figures 5,6; Plate 48, figures 1–5;

Plate 49, figures 1–6; Plate 50, figure 1

Pachyphyllum crassicosatum Webster, 1889, p. 623; Fenton and Fenton, 1924, p. 51, Pl. 8, fig. 1, Pl. 9, figs. 1–5; Sorauf, 1978, p. 827, Pl. 4, figs. 2–5.

Pachyphyllum owenense Webster and Fenton, in Fenton and Fenton, 1924, p. 50, Pl. 7, fig. 5.

Pachyphyllum cf. *P. crassicosatum* McLean, 1986, p. 448, figs. 48.32–48.33.

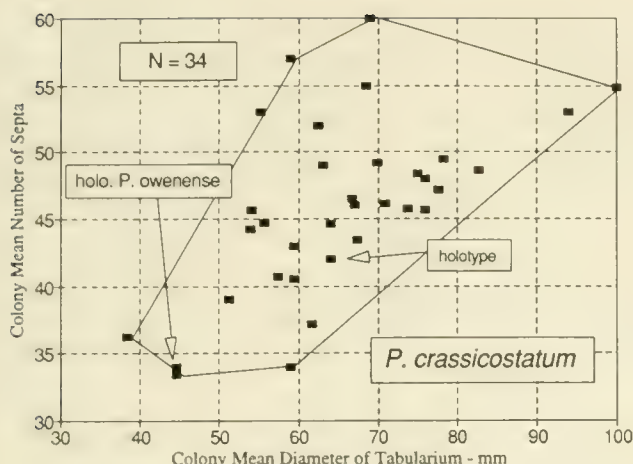
Pachyphyllum anfractum McLean, 1986, p. 447, figs. 48.28–48.31.

Diagnosis.—Large-diameter species of the genus with long major septa either joined at corallite axis or with irregular inner portion surrounding small open axial space. Septal trabeculae strong rhipidacanth with marked separation between laterally diverging trabeculae. Septa generally greatly dilated over sleeve of uniform horseshoe dissepiments; many (but not all) colonies with septa dilated into lateral contact with one another. Interior dissepiments present within sleeve of horseshoe dissepiments. Septa generally confluent between corallites. Tabularium with periaxial rows of saucer-shaped tabulae and characteristic wavy axial ends of septa seen interrupting tabulae in longitudinal section. Species sometimes occurs as colonies in which founder corallite has considerable length and has grown to mature diameter prior to budding.

Description.—*P. crassicosatum* generally occurs as compact thamnasteroid colonies with exsert corallites extending 6 to 9 mm above the general surface of the colony. This surface bears septal ridges that are largely confluent between corallites. At their greatest, these colonies have a diameter of approximately 18–20 cm. Some small colonies are characterized by having a long founder corallite with budding occurring only above the stalk-like, mature founder (Pl.3, fig.5).

P. crassicosatum colonies have large corallites, with colony means for tabularium diameter ranging from 3.9 to 10 mm for 34 colonies, with the colony mean number of septa varying from 34 to 59 (Text-fig. 45). These means vary somewhat with geography, as discussed below. In addition, these measurements are affected by the number of immature corallites within the colony. If *only* the largest corallite in each colony were considered, these would range from 4.0 to 11.2 mm, and have a mean of 7.5 mm in these 34 colonies.

Septa are clearly differentiated into major and minor series, with major septa commonly extending close to the axis of the corallite where they may join to form an axial boss or they may have an irregular form and terminate around a small open space (Pl.48, figs.1,4). This terminal irregularity is seen both in transverse (Pl.49, fig.2), and in longitudinal sections (Pl.49,



Text-figure 45.—*Pachyphyllum crassicostata* of the upper Owen Member, colony mean diameter of tabularium (in mm) plotted versus the colony mean for total number of septa in corallites. In addition to the holotype of this species shown on the graph, that of *Pachyphyllum owenense* Webster and Fenton is also shown, as it is considered to be a small diameter colony of *P. crassicostata*.

fig.5), and is characteristic for the species wherever the septa are long. Minor septa are somewhat unusual for the genus in that they may extend some distance past the horseshoe dissepiments rather than terminating at their inner margin. At the extreme, minor septa may extend as much as $\frac{1}{2}$ as far into the tabularium as do major septa. Septa all dilate at the position of the horseshoe dissepiments in the inner dissepimentarium and lateral divergence of rhipidacanth septal trabeculae is obvious in transverse sections. Extreme dilation (three to four times "normal" thickness) is seen in some colonies, with septa almost joining laterally over the horseshoes. At the other extreme, some colonies show relatively little dilation, so that less than $\frac{1}{2}$ the perimeter of the tabularium is occupied by septal stereome, and septa have a fusiform dilation, as so often seen in the genus and family. Septa are generally confluent between corallites (Pl.49, figs.1,2); budding, however, tends to disrupt confluency.

In longitudinal section, the structure within the tabularium often appears irregular due to interference between long major septa and tabulae (Pl.48, fig.5). Within colonies characterized by corallites with short septa, the central part of the tabularium is occupied by flat but irregular tabulae. Where septa are long and joined or nearly joined at the axis, periaxial rows of uniformly sagging tabulae commonly occur at the margins of the tabularium (Pl.49, fig.5). The irregular nature of the axial margins of septa can be seen in both transverse and longitudinal sections. There was a continued, irregular twisting of the axial portion of the polypal base during growth and skeletogenesis.

In longitudinal section are also seen the extreme rhipidacanth septal trabeculae. These are all widely spaced and isolated from one another by septal stereome over the horseshoe dissepiments (Pl.49, figs.3,4). Trabeculae can be seen bending away from a divergence line in the plane of the septum; where septa are dilated, trabeculae can be seen bending to the horizontal, thus perpendicular to the septal plane. In some specimens this has the appearance of small, carinae-like lateral extensions, covered smoothly by stereome (as seen in transverse sections); rhipidacanth does not extend beyond the lateral margins of the septa.

The dissepimentarium is marked by a very prominent and uniform row of horseshoe dissepiments that are secondarily thickened by stereome, commonly with a heavy coating of stereome on both the interior and exterior side of the horseshoes (Pl.49, fig.3). On their interior side there generally occur only one or two rows of steeply inclined normal dissepiments (Pl.48, fig.5). External to the horseshoes are seen elongate and flattened or small and somewhat globular dissepiments. Generally these layers of normal dissepiments arch upward to the horseshoes, reflecting the exsert nature of the calice, and this arrangement is reflected in the septal trabeculae which are vertically oriented between corallites and grade into fans over the sleeve of horseshoes at the margin of each corallite tabularium.

Type specimens.—Lectotype USNM 78628A, paralectotype USNM 78628 (here designated). *P. owenense* holotype is FMNH 25982 (erroneously listed as FMNH 26054 by Fenton and Fenton, 1924, p. 51), paratype is USNM 78627.

Discussion.—*P. crassicostata* is a large diameter, strongly exsert species of the genus. As such it is strongly reminiscent of the type species of *Pachyphyllum* Milne-Edwards and Haime (1851), who noted that this species, *P. bouchardi*, from the Boulonnais region of northern France, has corallites with diameters of 15 to 20 mm, which is about twice the diameter of the Iowa forms, and with exsert tabularia apparently extending 6 to 8 mm above the surface. *P. mirusensis* McLean (1986, p. 449) is apparently also a species of *Pachyphyllum* with larger sized tabularium than that of *P. crassicostata*.

Webster (1889, p. 623) did not illustrate or designate any types for the species. Later, Fenton and Fenton (1924, p. 52) noted that "cotypes" were in the "Collection of C.L. Webster". The specimens are now USNM 78628 and 78628A, each labeled "cotype". I here select USNM 78628A as lectotype; the second specimen, USNM 78628 is lectoparatype. The two specimens labeled "plesiotypes" by Fenton and Fenton (1924, p. 52) are regarded as topotypes. Locality

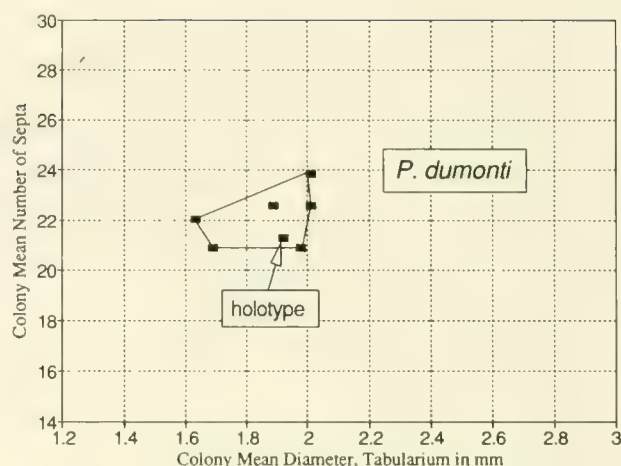
information on the type specimens is sketchy: "Owen Grove, Iowa". This is presumably Locality 25 (Appendix), on the west side of Owen Grove, along Owen Creek, which yielded numerous fine coral specimens to both Webster and Charles Belanski from the uppermost beds of the Owen.

Within the Iowa fauna, there are apparently two more or less distinct morphotypes, one with smaller diameter and somewhat fewer septa than the other. The sizeable collection of specimens from the Lillibridge Quarry (Locality 38) generally have larger corallites and contain many more septa than the population centered on specimens from the Morgan Quarry to the southeast. This may be environmental as well as biogeographic, as specimens collected from Owen biostromes in the Morgan Quarry are close to those from biostromes in the Lillibridge quarry. Colonies from Owen Grove can have large corallites with many septa, or be somewhat smaller, as is the lectotype of the species.

Pachyphyllum owenense Webster and Fenton, in Fenton and Fenton 1924, occurs within the population with small corallites, as noted above in *P. crassicos-tatum*, and is indeed smaller and has fewer septa than do the typical large corallites of colonies of the latter (Pl.45, fig.3). I consider the Webster and Fenton species to be synonymous with *P. crassicos-tatum* (Text-fig. 45).

P. crassicos-tatum has also been found in Frasnian rocks of New York State (Sorauf, 1978, p. 827), and the fauna there is remarkably similar to that of Iowa, although major septa tend to be slightly shorter and the colonies from New York appear to be more aphroid than do the Iowa ones. The species also occurs in Frasnian strata of western Canada. McLean (1986, p. 448) referred specimens to *Pachyphyllum* sp. cf. *P. crassicos-tatum*. My opinion, based on his published figures, is that these fit well into the Iowa species, although they are more aphroid than some. McLean's species *P. anfractum* (1986, p. 447) also fits within the range of variation in septal dilation and tabularium diameter present in the Iowa fauna of *P. crassicos-tatum* and is here synonymized. Additionally, it is also possible that *P. miniaceum* McLean (1986, p. 446) should also be placed within the Iowa species, but it is very regular in size, shape, and degree of septal dilation in corallites, moreso than those of the *P. crassicos-tatum* fauna in Iowa.

Occurrence.—*P. crassicos-tatum* is the typical upper Owen species throughout the northern area of outcrop. It is the thamnasterioid coral of the "Acervularia zone" of Fenton and Fenton (1924, p. 8), the term they used for the uppermost limestones of the member. *P. crassicos-tatum* does not occur in the upper Owen in



Text-figure 46.—*Phillipsastrea dumonti* n. sp. from the upper Owen Member, colony mean diameter of tabularium (in mm) plotted versus the colony mean for total number of septa in corallites. The holotype of this new species is indicated.

the most southerly area, where this uppermost unit is quarried, south of Dumont, Iowa. Here the species was apparently replaced by *P. dumonti*, characterized by very small corallite size. *P. dumonti* and *P. crassicos-tatum* occur together only in the Morgan Quarry (Locality 39, Appendix), which is situated between Lillibridge Farm Quarry (Locality 38), where *P. crassicos-tatum* was abundant, and more southerly quarries, where it was totally absent. *P. crassicos-tatum* was abundant in uppermost Owen beds at Owen Grove Quarry (Locality 26, Appendix), in the pasture along Owen Creek to the west (Locality 25), in these same beds at Rockwell (Locality 36), and formerly at Linn Grove Park in Rockwell (Locality 37), as well as occurring in great numbers at Lillibridge Quarry (Locality 38), as noted above.

***Pachyphyllum dumonti*, new species**

Plate 50, figures 2–5; Plate 51, figures 1–5

Diagnosis.—Small-diameter species of the genus with colony mean diameter of tabularium ranging from 1.6 to 2 mm. Long major septa generally 10 to 12 in number, extending to corallite axis and forming either weak columella or an aulos. Colonies are thamnasterioid to aphroid, with heavy dilation of septa over horseshoe dissepiments.

Description.—Colonies are large and massive, thamnasterioid to aphroid, and up to 40 cm in diameter and 10 cm in thickness.

In transverse section, the small corallite tabularium is characteristic, with colony mean diameter varying from 1.6 to 2 mm in seven colonies studied, while the mean number of septa per corallite varies from 21 to 24 in these same colonies (Text-fig. 46). The species

is more constant in diameter of tabularium and number of septa than are most other species of the genus.

Septal dilation at the outer margin of the dissepimentarium is marked and heavy, forming a massive sleeve in which dilated septa are in lateral contact (Pl.50, figs.2–4). This characteristic is somewhat variable, and some colonies show less septal dilation, still spindle-shaped, with septa which are distinctly separate (Pl.51, fig.1). In colonies where dilation is heavy, some areas have corallites with less dilation, and these are places where budding has been rapid and recent (Pl.51, fig.2).

Minor septa are short and do not enter the tabularium, while major septa are long. The long major septa in this species commonly form a small diameter aulos at the corallite axis (Pl.50, figs.3,4). This may be either a solid aulos or a somewhat irregularly formed columella. Septa are generally confluent between corallites, but all colonies are at least partly aphroid. Even in colonies with overall confluency, no corallites totally lack aphroid septa. Dilated portions of septa are spindle-shaped (Pl.51, fig.5).

In longitudinal section, septal rhipidacanthi form very tight fans over the horseshoe dissepiments at the outer margin of the tabularium. The horseshoe dissepiments themselves form a uniform sleeve, and at times are only seen with difficulty in thin-section due to their being masked by the extreme dilation of septa; thus, they are best seen where septa are more spindle-shaped (Pl.51, figs.3,4). The tabularium is dominated by the presence of the aulos, separating a row of flattish to slightly sagging axial tabulae from a periaxial series of uniformly sagging tabulae (Pl.51, fig.4). Dissepiments are generally small and numerous, with 12 to 15 rows between neighboring tabularia. Dissepiments are occasionally large and flattened, and tend to occur along horizons which parallel growth surfaces.

Type Specimens.—Holotype PRI 44820; paratypes PRI 44821, 44822, 44823.

Discussion.—Small-diameter species of *Pachyphyllum* (and/or *Phillipsastrea*) are common in North America. They all have characteristics in common with *P. dumonti*.

Phillipsastrea nevadense Stumm, 1940 is one such species from the Nevada Limestone in what was the White Pine Mining District in central Nevada. In Stumm's illustration (1940, p. 64, pl.8), the specimen shown has a small-diameter tabularium and long major septa apparently forming an aulos, although this was not mentioned in Stumm's description. The septal dilation in *P. nevadense* does not compare to that developed in *Pachyphyllum dumonti*; septa do join laterally, but barely so, as dilation is much more restricted and limited in area. The tabularium diameter ap-

proximating 3 mm is larger than that of *P. dumonti*, and its degree of septal confluency is also much greater.

Phillipsastrea exigua Lambe, 1901, as described by Smith (1945, p.42), from the MacKenzie River region of western Canada, is another small diameter species. It is smaller than *P. dumonti*, with the diameter of its tabularium approximately 1 mm and with fewer septa (16–20). In *P. exigua*, major septa are shorter than in the Iowa species, only just reaching into the tabularium, and the colonies are very strongly aphroid, with septa restricted to the immediate area around the tabularium. This is, however, a variable character, and some colonies in the Iowa fauna have tabularia completely free of septa, with septa more extensively developed in the dissepimentarium.

Pachyphyllum variabile (Sorauf, 1988) from the Sly Gap Formation of southern New Mexico is similar in several features to the Iowa species. In its size, length of major septa and the aulos sometimes present it resembles *P. dumonti*. The New Mexico species does not have the degree of septal dilation that *P. dumonti* does, and additionally, it is characterized by the breakdown of septa in the dissepimentarium into trabecular pillars marking septal paths.

Each of these species occurs in Frasnian rocks in the company of other species of the genus, one of which commonly resembles *P. woodmani*. In Frasnian strata of New York, two subspecies of *P. woodmani* have been recognized on the basis of corallite sizes. The smaller subspecies, *P. woodmani avocaensis*, has a complete range of size from those typical of the species to those typical of this eastern subspecies, with diameters in the 2 to 2.5 mm range. The smallest individuals of the New York subspecies resembles *P. dumonti*, with long septa forming an aulos and with similar septal dilation. It characteristically has more confluent septa than the Iowa species. *P. dumonti* has uniformly smaller-diameter corallites, and occurs in much younger rocks in Iowa.

Several colonies of *P. dumonti* have marked banding, appearing in transverse sections as rows of stereome coated and thickened septa connecting neighboring corallite tabularia (Pl.51, figs.1,2). This is a reflection of growth variation, and these dark bands apparently mark positions of slow growth at colony margins, as it is most obvious in the peripheral parts of the colonies. In one colony it is clear that such a growth line separates an area of more weakly dilated, aphroid corallites from a second area of corallites with more typically dilated, more confluent septa. Possibly two colonies have grown together along this boundary to form one large mass.

Occurrence.—*P. dumonti* is common in the upper-

most portion of the Owen Member, but only in the southern area of the Owen (in quarries). The holotype is from the uppermost 1.5 m (5.5 ft.) of the Owen at the Carrollus Quarry (Locality 41, Appendix). Other colonies have been collected from this same horizon in the Buseman Quarry south of Dumont, Iowa (Locality 40) and one specimen was found in the uppermost 0.6 m (2 ft.) of the Owen at the Morgan Quarry, near Airdale, Iowa (Locality 39). The species is thus restricted to the area in Townships 91 and 92 North, in Franklin and Butler Counties.

Etymology.—Named for the town of Dumont, Iowa.

Genus **TRAPEZOPHYLLUM** Etheridge, 1899

Trapezophyllum Etheridge, 1899, p. 32; Hill, 1939, p. 234; Glinski, 1955, p. 107; Schouppé, 1958, p. 228; Pickett, 1967, p. 31; Sorauf, 1972, p. 433; Hill 1981, p. F284; McLean, 1989, p. 242.

Sulcophyllum Pedder, 1963, p. 366.

Type Species.—*Cyathophyllum elegantulum* Dun, 1898.

Diagnosis.—Cerioid phillipsastreid genus characterized by rhipidacanth septal trabeculae in well-developed, symmetrical fans and uniform sleeve of horseshoe dissepiments, generally with stereome rather heavily deposited on both septa and horseshoes. Row of flat, ladder-like dissepiments often present in corallite periphery. Colonial form diagnostic for the genus, with truly cerioid walls (epithecal) separating corallites.

Discussion.—Published data on *Trapezophyllum* focuses on Australian and German Middle Devonian species. As proposed by Etheridge, and illustrated by Hill (1939), Glinski (1955), Schouppé (1958), Pickett (1967), Sorauf (1972) and others, the genus has been regarded as a phillipsastreid in the narrow sense, with rhipidacanth septal trabeculae in fans centered over a sleeve of horseshoe dissepiments, and with distinctive flat dissepiments seen in longitudinal section as a single row peripheral to the horseshoes. The genus has a truly cerioid colonial form, with an epithecal wall separating corallites. Seen in longitudinal section, the ladder-like row of dissepiments separates the horseshoe dissepiments from the epithecal wall. This distinctive genus, with dissepimental "ladders" is known from Lower and Middle Devonian rocks of Australia, Germany and China (Hill, 1981, p. F284), and from Washington State in North America (Sorauf, 1972). The stratigraphic position of the Washington material is questioned by new data on the age of Devonian rocks at Limestone Hill in northeastern Washington, once regarded as composed solely of Middle Devonian carbonates, but now known to contain Frasnian strata as well (McLean and Pedder, 1987, p. 158). There is also an undescribed species of *Trapezophyllum* in the Fras-

nian Martin Limestone of Arizona (McLean and Sorauf, 1989, p. 390).

In Hill's 1981 revision of the Rugosa, she figured topotypic material of the type species of *Trapezophyllum*, *T. elegantulum* (Dun), and showed clearly that this species is characterized not just by ladder-like dissepiments, but also that, "In some the flat dissepiments are replaced by a few series of abaxially declined or subhorizontally based globose dissepiments" (Hill, 1981, p. F284). Thus, the genus concept is broadened considerably, as cerioid phillipsastreids with flat outer dissepiments or with some globose dissepiments, can both be placed in the taxon. In Hill's photographs of topotypes of *Trapezophyllum elegantulum* (1981, fig. 183, 2a-c), longitudinal sections are shown with numerous normal dissepiments external to the horseshoe dissepiments, with the outer, ladder-like dissepiments only occupying the peripheral position. This broadened definition of the genus embraces the specimen described here from the Shell Rock Formation of Iowa. It also makes the genus *Sulcophyllum* Pedder a junior synonym of *Trapezophyllum*. In Pedder's description of his genus he stated, "In its possession of outer flat dissepiments *Sulcophyllum* resembles *Trapezophyllum* which is also cerioid, but there is no zone of outwardly convex dissepiments between the horseshoe and flat dissepiments in *Trapezophyllum*" (1963, p. 366). Since normal, convex dissepiments are now known to be abundant in the type species of *Trapezophyllum*, there is no reason to retain the additional genus name. The existence of normal dissepiments in the topotypes figured by Hill and the relationship with *Sulcophyllum* also have been discussed thoroughly by McLean (1989, p. 242).

The genus *Smithicyathus* was proposed by Rozkowska (1980, p. 18), based on the type species *S. cinctum* Smith 1945, from western Canada. *S. cinctum* is characterized especially by aphroid septa, with cerioid walls enclosing more than one corallite and with walls lacking between the enclosed aphroid individuals. It is of very late Frasnian age. The Shellrock specimen shows neither the tendency toward aphroid corallites, nor does it enclose multiple corallites within its cerioid walls. It does, however, develop a subphaceloid form that was also cited as typical for *Smithicyathus* (Rozkowska, 1980, p. 18), but perhaps has an ecological origin, as a response to sediment accumulating adjacent to the coral polyps.

Trapezophyllum species A

Plate 52, figures 1–3

Description.—This colony is cerioid. Not only does it have an epithecal (three-layered) wall, but these walls separate all corallites in the colony. A few cor-

allites grow free from the upper surface of the massive colony, and these also have an epithecal wall, which is commonly abraded away, perhaps due to its thinness.

In transverse sections, corallites range in size from 4.0 to 5.8 mm for the diameter of tabularium and contain 38 to 46 septa in two series. Mature-appearing corallites in this colony have tabularium diameters that range from 4.9 to 5.8 mm, and have 42 to 46 septa equally divided into major and minor septa, with all 21 to 23 minor septa developed. Septa show spindle-shaped dilation as typical for the family, expanding laterally at the outer margin of the tabularium to occupy $\frac{2}{3}$ to $\frac{3}{4}$ of the space over the horseshoe dissepiments (Pl.52, fig.1). Horseshoe dissepiments are themselves heavily coated with stereome; thus the sleeve of horseshoes is clearly defined (Pl.52, fig.3). Septa are complete and straight in the outer dissepimentarium, and abut straight, epithecal walls at a high angle.

In oblique and longitudinal sections, rhipidacanth septal trabeculae can be seen forming tight symmetrical fans over the vertical row of uniform horseshoe dissepiments. Stereome thickens these dissepiments on both the inner and outer side. Mature, large diameter corallites have four to six rows of flattened normal dissepiments in the outer dissepimentarium, but several smaller individuals have only a single row of flat dissepiments. One corallite has two rows of "normal" dissepiments, then one row of flat dissepiments at its periphery (Pl.52, fig.2). Tabulae tend to be irregular to almost complete and form a flat base to the calicinal pit. Most commonly there are large incomplete tabulae, inclined adaxially, located at the periphery of the tabularium.

Discussion.—This single colony is placed in the genus *Trapezophyllum*, since the dissepimentarium is variable, and not dissimilar to that illustrated from topotypes of the type species of the genus by Hill (1981, p. F284). The subphacelloid nature of the uppermost corallites of the colony is regarded as an ecologic response to rapid sedimentation, which finally caused the death of the colony.

The Iowa colony of *Trapezophyllum* does not closely resemble the undescribed species of the genus in the Frasnian Martin Limestone of Arizona (McLean and Sorauf, 1989, p. 390). The latter has more closely packed corallites, and has a uniform ladder-like configuration of outer, flat dissepiments at the periphery of the corallite, external to the row of horseshoe dissepiments.

Other Frasnian colonial phillipsastroid corals with a truly cerioid colonial form are placed in the genus *Smithicyathus* Rozkowska, 1980. These are known from late Frasnian strata in the Northwest Territories

of Canada (*S. cinctum* [Smith]) and in Poland (*S. lubliensis* Rozkowska). The former is a species with very small-diameter corallites and strikingly aphroid septa within cerioid walls, while the latter is somewhat larger, but with short septa likewise separated from the walls by a lonsdaleoid dissepimentarium.

Occurrence.—The single colony of this species collected came from float covering the basal, shaley beds of the Mason City Member in the abandoned quarry northwest of Marble Rock, Iowa (Locality 23, Appendix). It most likely came from the upper Mason City beds at this locality, where two colonies of *Pachyphyllum minutissimum* were collected.

Genus **MACGEEA** Webster, 1889

Pterorrhiza Ehrenberg, 1834, p. 312 (nomen oblitum); Pickett, 1967, p. 27; Birenheide, 1969a, p. 42; Birenheide, 1969b, p. 121; Birenheide, 1978, p. 108; Hill, 1981, p. F286; Birenheide and Soto, 1992, p. 111.

Macgeea Webster, 1889b, p. 710; Fenton and Fenton, 1924, p. 53; Lang and Smith, 1935, p. 552; Stainbrook, 1946, p. 419; Rozkowska, 1953, p. 18; 1956, p. 288; 1957, p. 102; Schouppé, 1958, p. 220; Stumm, 1962a, p. 161; Schouppé and Stacul, 1963, p. 266; Schouppé and Cheng, 1969, p. 171; Brice and Rohart, 1974, p. 47; Coen-Aubert, 1982, p. 14; McLean, 1984, p. 472; Sorauf, 1988, p. 172; McLean, 1989, p. 244; Coen-Aubert and Wrozelek, 1991, p. 10.

Pexiphyllum Walther, 1928, p. 128; Birenheide, 1978, p. 112; McLean, 1989, p. 245; Birenheide, 1990, p. 270.

Trigonella Rozkowska, 1980, p. 24.

Debnikiella Rozkowska, 1980, p. 25; McLean, 1989, p. 245.

Rozkowskaella Wrozelek, 1987, p. 277.

Type Species.—*Pachyphyllum solitarium* Hall and Whitfield, 1873, Lime Creek Formation, Upper Devonian, Iowa.

Diagnosis.—Corals solitary or with few buds, characterized by everted calice, with prominent septal ridges above lower collar of epitheca; radial septa with variation ranging to having septa in distinct quadrants. Major and minor septa with symmetrical fans of rhipidacanth trabeculae and marked dilation of septa in inner dissepimentarium. Well-developed sleeve of horseshoe dissepiments located at axis of divergence of trabecular fans, with horseshoes commonly thickened by stereome or covered by stereome containing rhipidacanth from adjacent septa. Normal dissepiments are seen interior to, and less commonly exterior to, the row of horseshoe dissepiments, with peripheral development of flat dissepiments. Septal ridges present on upper part of corallum, representing polypal edge zone above epithecal sheath.

Discussion.—The synonymy provided above shows modern usage. Since 1967, a dichotomy has developed in the manner of usage of the genus name, but *Macgeea* Webster, 1889 is properly used, rather than *Pterorrhiza* Ehrenberg 1834. The name *Pterorrhiza* Ehren-

berg 1834 was first mentioned for the second time in a faunal list by Sanford in 1939 (p. 409), more than 100 years later. It thus was a *nomen oblitum*. Lang *et al.* (1940, p. 111) were correct in regarding it as lapsed. They chose as lectotype of the type species, *Cyathophyllum marginiferum*, noted that it had been lost and stated that "The genus therefore lapses". Pickett (1967, p. 27), utilized the name *Pterorrhiza* for the genus, as have Birenheide (1969a, p. 42, 1978, p. 108), Rozkowska (1980, p. 20), Hill (1981, p. 286), and Birenheide and Soto (1992, p. 111), regarding it as the senior synonym of *Macgeea*. This is incorrect, as the International Code of Zoological Nomenclature specifically requires that a *nomen oblitum* not be used without the Commission's approval (1985, p. 175, article 79c). Schouppé and Cheng (1969) rightly argued for suppression of the name *Pterorrhiza*; this was supported by Pedder (1969) and by Pickett (1969) and opposed by Birenheide (1969b, p. 121). The Commission has not acted on the matter. Following Article 79(c) of the 1985 edition of the Code, the name *Macgeea* is used here.

Extended discussions of the genus were provided by Schouppé and Stacul (1963, 1966) and Brice and Rohart (1974). The former provided an exhaustive summary of previous work, skeletal structure and nomenclature, and the latter authors presented an extended discussion of morphology and definition of the genus. Brice and Rohart (1974, p. 48) also noted that the genus is characterized by a tripartite dissepimentarium with horseshoe dissepiments separating outer, flattened dissepiments from inner dissepiments that are axially inclined. They stated additionally that the genus is generally solitary, but that in some species, specifically *Macgeea gallica*, minor budding does occur in mature solitary corallites. Coen-Aubert and Wrzolek (1991) followed the definition of the genus of Brice and Rohart. They have defined two subgenera, based on the manner of development and persistence of horseshoe dissepiments. They defined *Macgeea* (*Macgeea*) as having horseshoe dissepiments in adult corallites, while *Macgeea* (*Rozkowskaella*) only has horseshoe dissepiments when immature (1991, p. 10). This basis for division of *Macgeea* into subgenera might be questioned, but it does not affect the taxonomy of Lime Creek and Shell Rock corals, as all species present here fit well into the nominate subgenus. Schouppé had previously defined subgenera within this group on the basis of their solitary or colonial form, putting solitary corals in *Macgeea* (*Macgeea*) and fasciculate corals into *Macgeea* (*Thamnophyllum*) (1958, p. 226). Coral specialists all have since treated these two taxa as separate genera (Hill, 1981, p. F289).

Birenheide (1978, p. 112) regarded the genus *Pex-*

iphyllum Walther as separate from *Macgeea* (or *Pterorrhiza*, which he regarded as the appropriate genus name for the group). He placed most of the species described by Rozkowska (1953) as *Macgeea* into *Pexiphyllum*, although noting that it is difficult to separate the two genera, but that *Pexiphyllum* is only typically developed in the Frasnian. Thus Birenheide apparently distinguished the the genus by its age. This grouping of Frasnian species of *Macgeea* into *Pexiphyllum* was not acceptable to Coen-Aubert (1982, p. 14), and is not acceptable to me.

The genera *Trigonella* and *Debnikiella* were proposed by Rozkowska (1980, pp. 24 and 25, respectively). The former is based on a single specimen that is triangular in outline, and apparently lacking in horseshoe dissepiments in its mature stage (1980, p. 24), while the latter was based on one fragmentary coral also lacking a uniform row of horseshoe dissepiments in its dissepimentarium. Since the former is a homonym of a bivalve species, Coen-Aubert and Wrzolek (1991) treated this as the subgenus *Rozkowskaella*, a name substituted by Wrzolek (1987) for *Trigonella*, and placed *Debnikiella* into synonymy with *Rozkowskaella* (Coen-Aubert and Wrzolek, 1991, p. 10). McLean (1989, p. 245) had previously placed both *Trigonella* and *Rozkowskaella* into synonymy with *Debnikiella*. This does not involve the Iowa faunas, as all *Macgeea* species from Iowa are central to the genus and/or a nominate subgenus.

An excellent review of European species of *Macgeea* is presented by Brice and Rohart (1974), and species from Belgium are well defined by Coen-Aubert (1982). McLean (1989) has discussed the genus in western Canada, and Sorauf (1988) dealt with a New Mexican species of *Macgeea*.

Distribution.—The distribution of the genus *Macgeea* is virtually that of the cosmopolitan faunas of the Givetian and Frasnian, with diverse species reported from England, France, Belgium, Germany, Spain, Poland and Russia in Europe, from the United States and Canada in North America and from Algeria in Africa, as well as numerous occurrences in Asia.

Macgeea solitaria (Hall and Whitfield, 1873)

Plate 52, figures 4–8; Plate 53, figures 1–23; Plate 54, figures 1–9, Plate 55, figures 1–5

Pachyphyllum solitarium Hall and Whitfield, 1873, p.232. Pl. 9, figs. 6–8.

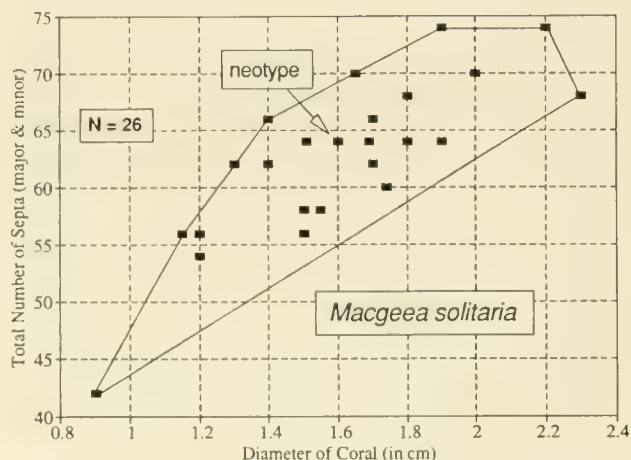
Macgeea solitaria Webster, 1889, p. 711; Fenton and Fenton, 1924, p. 54, Pl. 9, figs. 7–10; Lang and Smith, 1935, p. 552, text-figs. 10,11, Pl. 37, figs. 1–3; Smith, 1945, p. 27, Pl. 24, fig. 1; Stumm, 1949, p. 35, Pl. 17, figs. 1–3; Stainbrook, 1946, p. 420, Pl. 57, fig. 16, Pl. 60, figs. 11,14; Coen-Aubert and Wrzolek, 1991, p. 8, Pl. 1, figs. 1–3.

Pterorhiza solitaria Pickett, 1967, p. 65, Pl. 5, figs. 19–21.
not *Macgeea solitaria* Tsien, 1969, p. 70, Pl. 48, figs. 7,8,16.

Diagnosis.—Variable, small- to medium-sized, solitary trochoid to subcylindrical corals with long, subradial major septa; characteristic tripartite dissepimentarium, generally with two to four rows of steeply inclined internal dissepiments; well-developed and uniform horseshoe dissepiments thickened by stereome, accompanied by marked septal dilation in the inner dissepimentarium, and with generally flat, but sometimes irregular or globose peripheral dissepiments. Septal trabeculae rhipidacanth, forming tight, symmetrical fans that are centered on the sleeve of horseshoe dissepiments. Individual corals commonly have distorted base reflecting larval settling on hard substrate and molding to it.

Description.—*M. solitaria* is a small- to medium-sized coral with an ovoid or angular, sometimes almost triangular cross sectional outline, in external view characterized by exsert septa exposed above very thin epitheca, which is commonly absent in rings around the exterior of the corallite (Pl.52, figs.4–8). The specimen figured by Hall and Whitfield was roughly triangular in outline (1873, Pl. 9, fig. 7), and this is shown by a number of other specimens (Pl.53, figs.2,7,10). As in other species of the genus, the corallite is characterized by a calice with a deep, flat pit and septa standing high above the surrounding epitheca. The corals also commonly have a deformed base where larvae settled on, and conformed to, a hard substrate such as brachiopods, bryozoans or other corals.

In transverse section *M. solitaria* ranges in average diameter from 9 to 22 mm, with a mean of 15 mm for 28 specimens. Adult diameters are mostly in the 18 to 22 mm range (Text-fig. 47). Septa are subradially arranged and differentiated into major and minor orders, with a cardinal septum sometimes identifiable. Major septa number 27 to 38 in the 28 individuals noted above. Larger forms have 32 to 37 major septa. Major septa are long, reaching to the axis of the corallite or leaving a small open area (<4 mm). Septa either have an irregular trace in the tabularium, or more commonly, may bend to swirl around a small axial open space. Major septa are dilated over the horseshoe dissepiments and are thin throughout the tabularium, sometimes dilating slightly in the axial area. When an axial open space is present, this is elongate, thus parallelling the ovoid external shape of the corallite (Pl.54, fig.7). Major septa of some corals extend to the axial plane of corallite elongation and stop there without joining (Pl.54, figs.1,4). Minor septa are short, at most extending only slightly into the tabularium and their inner margin is generally near the inner margin of the



Text-figure 47.—*Macgeea solitaria* from the upper units of the Cerro Gordo (formerly called the “*Spirifer* zone”), diameter of corallite (in mm) plotted versus the total number of septa for each individual studied. The proposed neotype (U.S.N.M. 48449a) is indicated on the graph.

row of horseshoe dissepiments, itself always thickened by the addition of stereome. It is usual to see intersections of two or three rows of steeply dipping dissepiments interior to the horseshoe row and lateral to the axial margin of the minor septa (Pl.54, fig.6).

In longitudinal section, the horseshoe dissepiments and fan of rhipidacanth septal trabeculae centered over the horseshoes are prominent features of the species. The tabularium is generally broad and filled with flat, usually complete tabulae, but is somewhat variable, often dominated by flat, very thick tabulae which occur at regular intervals, with less complete, slightly sagging or slightly arched tabulae in between. In some specimens, every sixth or seventh tabula is greatly thickened by stereome (as in Pl.55, fig.5).

The dissepimentarium is dominated by the presence of a sleeve of horseshoe dissepiments, so that longitudinal sections have a row on each side of the tabularium. Horseshoes are variable in that both shape and size can change within individuals. When the horseshoes are small, they tend to be very uniform in size and shape (Pl.55, fig.1), but when larger tend to vary much more in the arcuate nature of the dissepiment, in the position of the horseshoe relative to its neighbors above and below (Pl.54, fig.9), and in the size of the horseshoe as compared with its suprajacent neighbors (Pl.55, fig.4). The innermost part of the dissepimentarium characteristically has normal dissepiments interior (axial) to the horseshoe dissepiments (Pl.55, figs.4,5). These vary somewhat in number and in shape. They are steeply inclined or vertical and occur in two to four rows, depending on the length of the minor septa, as interior dissepiments occur only be-

tween minor and major septa. External to horseshoe rows are additional dissepiments, which may be flat and appear as a series of ladder-like peripheral dissepiments, or which may be globose and irregular, forming a more normal-appearing external dissepimentarium. These can also separate the ladder-like dissepiments from the rest of the outer corallite (Pl.54, fig.5).

Septal structure is typical for the genus, with a fan of coarse rhipidacanth septal trabeculae positioned with its axis of divergence centered over the horseshoe dissepiments. The rhipidacanth is directed laterally, as shown in transverse section, and contribute to the coating of the row of horseshoes seen in longitudinal section (Pl.55, fig.5).

Type specimens.—Neotype USNM 48449a (here designated), neoparatypes are USNM 135374, 135381, 2273b, 78449d, 78449f, 32706a, 32706b and 32706d.

Discussion.—*Macgeea solitaria* is a widely reported species of Frasnian corals. Illustrations of topotype specimens have been published by a number of authors: Fenton and Fenton (1924, pl.9, figs.7–10), Lang and Smith (1935, p. 552, Text-figs.10,11), Smith (1945, pl.24, fig.1), Stainbrook (1946, pl.57, figs.16; pl.60, figs.11, 14), Pickett (1967, pl.5, figs.19, 20), and Coen-Aubert and Wrzolek (1991, pl.1, figs.1–3). In none of these cases, however, has a population been studied or population variation evaluated. It has been known for a number of years that the holotype of the species was lost; a neotype is here proposed for the species (USNM 48449a; Pl. 52, fig.7; Pl. 53, figs.1–3).

There is a broad tabularium in this species, thus septal dilation occurs in a peripheral position. This can be exaggerated by erosion of the peripheral part of the dissepimentarium, so that the horseshoe dissepiments appear to be positioned right at the periphery. Tabulae also vary. They can be complete and flat, irregular where interfered with by septa, or incomplete in individuals with very long septa. Septal dilation can be extreme, so that at times septa touch each other laterally, or only leave a very small space for horseshoe dissepiments and stereome. This is also the area where septal rhipidacanth diverge from the axial plane of the septa, and appear in longitudinal thin sections as laterally directed, rounded rods, perpendicular to the plane of the thin section (Pl.55, fig.2).

The configuration of the outer dissepimentarium is reminiscent of the genus *Trapezophyllum*, in which dissepiments external to the horseshoe dissepiments may either be a series of flat, ladder-like platforms, or more irregular, as rows of somewhat more inflated dissepiments forming the platforms. This was not recognized in the genus *Trapezophyllum* until Hill (1981, p. F284) restudied topotypes of the type species of the

genus. The variation seen in *M. solitaria*, in which the outer dissepiments (as seen in longitudinal section) most commonly are uniform and ladder-like or somewhat irregular, or even replaced at some horizons by globular “normal” dissepiments, has not previously been described in *Macgeea solitaria*. This variation is often not easily seen, as weathering of specimens tends to remove the external dissepiments. Rapid lateral expansion of the dissepimentarium (Pl.54, fig.9; Pl.55, figs.1,2) appears to be connected with the formation of multiple rows of normal external dissepiments, probably associated with the polyp expanding its base rapidly outward, perhaps to avoid smothering by soft sediment.

Variation also occurs in horseshoe dissepiments. They may be developed as a relatively straight row of uniformly developed horseshoes, or may be a more irregular row; they may consist of dissepiments which vary in how arcuate they are and also vary somewhat in size. In the Iowa fauna, horseshoe dissepiments are almost invariably coated with stereome. This coating of stereome can be very heavy, and extend right on across the tabulae from one side to the other. In one specimen (Pl.55, fig.5), this is seen to occur at regular intervals within the corallite and perhaps is seasonal in origin.

Macgeea solitaria varies greatly, so much that some individuals of the Iowa species can be found which resemble individuals of many other species of the genus. Thus, it is extremely difficult to assess relationships between it and other species. The amount of variation illustrated on Plates 53 and 54 make this point clearly. There are however, recognizable differences between *M. solitaria* and other Frasnian genera from other outcrop areas. *M. gallica* from the Boulonnais region of France and related species are larger than *M. solitaria* (approximately 35 mm maximum diameter versus 22 mm for the latter), and contain considerably fewer septa than the Iowa species. *M. bathycalyx* of Germany and Poland is characterized by short septa and complete tabulae, while *M. dubia* of the Boulonnais is much smaller in diameter, with less than one-half the number of septa, thus both are easily distinguished from the type species. *M. multizonata* of Poland and Belgium has approximately the same diameter and number of septa as *M. solitaria*, but has consistent stereome thickening of the horseshoe dissepiments and a larger number of internal dissepiments than the latter. The occasional budding of adults, resulting in a smallish “colony”, with a long parent corallite and several small buds (Brice and Rohart, 1974, p. 53) is seemingly a major characteristic of the species *M. gallica*.

Macgeea camplanulata of the Owen Formation dif-

fers from *M. solitaria* by its more numerous internal dissepiments, its common bilaterality and its dilation of septa in the axial region, where uniformly long major septa swirl around the corallite axis and are dilated at their tips.

Occurrence.—The species was collected from the upper part of the Cerro Gordo Member of the Lime Creek Formation, and found at most localities where these beds outcrop. These were localities 27 and 27a, South Portland; 28, Type Lime Creek; 29, County Line Road North; 30, Bird Hill North; 31, Bird Hill; and 35, Rockford Brick and Tile Co.

***Macgeea camplanulata*, new species**

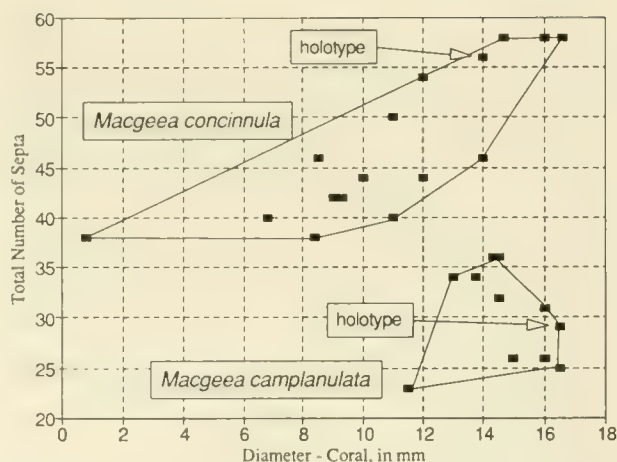
Plate 56, figures 1–12

Diagnosis.—Small, straight to slightly bent, trochoid solitary corallites with long septa reaching to the axis, and well-developed, steeply inclined internal dissepiments. Septa strongly dilated over row of horseshoe dissepiments, with outer dissepimentarium variously developed and generally only fragmentarily preserved. Tabularium most commonly filled with irregular complete and incomplete tabulae.

Description.—*Macgeea camplanulata* generally has small corallites with an ovoid outline, with maximum lengths near 25 mm and maximum diameter, above the calicinal pit, of 22 to 25 mm. Some are more elongate than others, and do not show apical attachment scars; thus it appears that they lived unattached on the sea floor or partially buried.

In transverse section, 11 specimens show a range in diameter of from 12 to 17 mm, with a mean of 15 mm, while for the same specimens, the total number of septa ranged from 46 to 72. The smaller corals with few septa are immature (Text-fig. 48). Diameters measured on transverse thin sections generally do not reflect the true size of these corals, as virtually all of them have undergone some unknown amount of erosion on the sea floor prior to burial. Thin epitheca and at least part of the weak outer dissepimentarium has been removed. Diameters here more accurately reflect the diameter of the corals as measured at the outside of the horseshoe dissepiments. These, thickened by stereome and more resistant to erosion than the weaker external dissepiments commonly form the outer surface of abraded coral specimens.

Septa are long and uniformly dilated in the inner dissepimentarium over the horseshoe dissepiments as in other species of the genus. Variation in these two features is common, and dilation varies, thus septa are dilated to fill between $\frac{1}{3}$ and $\frac{2}{3}$ of the space over the horseshoe dissepiments. Length of septa varies slightly; major septa usually extend nearly to the axis where they may swirl, leaving a small open area, or they may



Text-figure 48.—*Macgeea concinnula* n. sp. from the Nora Member, and *Macgeea camplanulata* n. sp. from the Owen Member, diameter of corallite (in mm) plotted versus the total number of septa for each individual studied. The holotype of each is indicated on the graph.

extend right to the axis and join the other septa (Pl.56, figs.1,3,6,7). When this happens, there commonly is a swollen tip to the septa. In one specimen, septa are joined at the base of the calicinal pit to form an axial boss. Minor septa are long, extending well beyond the horseshoe dissepiments, with intersections of four to five internal dissepiments seen between septa. The arrangement of septa is commonly somewhat pinnate (Pl.56, figs.3,11), and in two of the specimens studied, the cardinal septum is short and more prominently dilated than other septa are, with a weakly pinnate arrangement of other septa around the axial plane of the corallite.

In longitudinal section, up to eight rows of steeply inclined internal dissepiments are noted, although the usual development is four or five rows (Pl.56, fig.9). One specimen had none in its younger portion, then only several rows in the mature part of the section; thus this feature seems related to age. Horseshoe dissepiments are somewhat variable, but always thickened by stereome. They may form a straight row of uniformly sized and uniformly arched dissepiments or these may be much less regular, especially in the most mature part of the corallite where many internal dissepiments are also developed. Erosion of these corals very commonly has worn away the more exterior part of the dissepimentarium so that outer dissepiments are not seen. Where some of these are present, they are flat and ladder-like, but at least in the young part of the holotype, the flat broad base is filled with a multitude of small, steeply dipping, subarcuate dissepiments. This appears analogous to the development of talons in other rugosans as a way to spread on a hard

substrate, as evidenced by the impressions of brachipods or other shells in this early post-larval portion of the corallite.

The tabularium is quite irregular, in part at least due to the interference of long major septa with the building of tabulae. Tabulae are almost always incomplete, and may be flat or inclined, irregular, or together form a flat bottom to the calicinal pit. In one specimen, where septa were somewhat shorter and an open space was present at the corallite axis, there was developed a flat-topped, cap-like row of axial tabulae.

Septal trabeculae are discrete, separate rhipidacanth (Pl.56, fig.10).

Type Specimens.—Holotype SUI 3490, paratypes PRI 44826, 44827, 44818.

Discussion.—*M. camplanulata* of the Owen is similar to *M. solitaria* in size and in general shape, but has a much greater development of internal dissepiments and fewer and longer septa than does the latter. Since *M. solitaria* is highly varied in many characteristics, however, it is possible to find resemblances between individual corallites.

In its development of a multitude of internal dissepiments, *M. camplanulata* resembles several species seen in western Europe, especially *M. gallica gigantea* Brice and Rohart, 1974, and *M. multizonata* Read, 1922. *M. gallica* is much larger, with more internal dissepiments and has a greater number of septa (Brice and Rohart, 1974, p. 56) and *M. multizonata* is characterized by a consistent development of normal dissepiments in the interior part of the external dissepimentarium, inside the flat dissepiments at the periphery of the corallites (Coen-Aubert, 1982, p. 15).

Occurrence.—This *Macgeea* species is common in the Owen Member. It occurs along with *Pachyphyllum crassicostatum* in the upper part of the member, in the so-called "Acervularia zone", the uppermost beds of the member. Belanski collected the holotype in Owen Grove (Locality 26, Appendix). In the present study it was collected at Lillibridge Quarry (Locality 38), Buseman Quarry (Locality 40), North Buseman Quarry (Locality 40A), and Morgan Quarry (Locality 39).

Etymology.—This name was on a label in the Belanski collection, without explanation.

***Macgeea concinnula*, new species**

Plate 57, figures 1–11

Diagnosis.—Small, cylindrical to medium-sized, ceratoid corals of the genus with short, very heavily dilated septa; complete or incomplete flat tabulae, somewhat non-uniform row of greatly thickened horseshoe dissepiments. Internal dissepiments few or lacking, and variable external dissepimentarium with

flat, ladder-like peripheral dissepiments. Occasional corals have irregular dissepiments.

Description.—*M. concinnula* is composed of corallites with an external shape varying between two extremes, one with a small diameter, straight sides and cylindrical shape, and the other with a larger diameter and slightly ceratoid shape. Their diameters range from 7 to 17 mm in 16 specimens available for study, with a mean of 11 mm. Septa range from 38 to 58 with a mean of 47.1 in the same 16 individuals (Text-fig. 48). Septa are short, and major septa generally do not extend far into the tabularium. It is typical for corals in this species to have an axial open space of $\frac{1}{3}$ to $\frac{1}{2}$ the diameter of the tabularium, with straight septa terminating in the tabularium without swirling around the axis (Pl.57, figs.1,4). Septa are very heavily dilated at the horseshoe dissepiments, and this may form a uniform collar around the tabularium (Pl.57, figs.8,9). Cylindrical corals have smaller diameters (7 to 11 mm), a small number of septa (36 to 46), and all have a complete collar of stereome around the inner tabularium, formed of dilated septa and stereome coating, while those corallites with somewhat larger diameter (11 to 17 mm), may have more numerous septa (50 to 58), which are less dilated but may have very heavy coating of stereome restricted to the inner side only of the horseshoe dissepiments. Some specimens have a complete wall of stereome, which coats both septa and the internal flank of the horseshoe dissepiments. Minor septa are very thick also, but barely extend into the tabularium.

In longitudinal section, the species is distinctive in its complete, flat or sagging tabulae and accessory, incomplete tabulae. Typically, the species has a flat-bottomed tabularium, with tabulae sometimes complete, thin, and widely spaced (Pl.57, fig.8). Internal dissepiments are generally few and can even be missing, so that the transition from tabularium to dissepimentarium is very abrupt. One specimen, however, has the singular development of numerous normal dissepiments occurring inside, and almost merging with, the horseshoe dissepiments which are themselves rather irregular (Pl.57, figs.3,11). Horseshoe dissepiments usually form an orderly sleeve of uniformly sized, arcuate dissepiments, but can also be irregular. One specimen shows these two conditions on opposite sides of the same corallite. External dissepiments are rarely preserved as they are thin and easily eroded from corallites, but are well shown in the ladder-like configuration in one paratype (Pl.57, fig.9). In the immature part of one corallite, there is a marked development of normal, arcuate dissepiments outside the poorly differentiated horseshoe dissepiments (Pl.57, figs.7,8). The occurrence of these dissepiments, and also the great de-

velopment of very numerous internal dissepiments developed in one mature part of another corallite shows the variability common both in this species and in the genus. In these specimens (as in other Lime Creek and Shell Rock material), the periphery of the corallite is commonly weathered so that the preserved outer margin of the coral is either the horseshoe row or the internal dissepiments. Only in one specimen is the outer portion of the dissepimentarium well preserved, and here the outer dissepiments are ladder-like (Pl.57, fig.9).

Rhipidacanth septal trabeculae form symmetrical fans within heavily dilated septa and in heavy stereome deposited over horseshoe dissepiments. Where dilation and stereome are thickest, fans form continuous, dense coverings for horseshoe dissepiments (Pl.57, figs.8,9,11).

Type Specimens.—Holotype SUI 1257, paratypes SUI 1252, 1256, 1258, and 1275.

Discussion.—This group of corals presents something of a taxonomic dilemma, as the two extreme corallite shapes, taken by themselves, could be used to indicate separation of species. Cylindrical corals almost invariably have a complete ring of dilated septa and stereome at the position of the horseshoe dissepiments, and have fewer septa, perhaps as a result of their smaller diameter. Ceratoid corals almost invariably have a larger diameter and more septa than cylindrical ones, and in this larger coral, the dilated septa commonly do not form a solid ring around the tabularium. There is always a very heavy coating of stereome on the inner margin of the horseshoe dissepiments, and in both forms the minor septa almost never extend inside the ring of stereome. Again, in cylindrical forms the minor septa are generally (but not invariably) hidden within the solid ring of dilation and

stereome, and only extend an extremely short distance inside this sleeve. Accompanying this feature is a sharp boundary between the tabularium and dissepimentarium. Where there are short minor septa and a heavy collar of stereome, there usually are few or no internal dissepiments. There are exceptions to this generalization. There apparently is a continuum in maximum diameter, shape, and number of septa between corallites with cylindrical and ceratoid form; as a result, both are placed within this species. The difference does not seem to be biogeographical, as both forms occur together within the uppermost part of the lower biostrome of the Nora Member. Some individuals are attached to solid substrate, generally another coral, and these developed in the greatly elongate cylindrical growth form while forms without signs of attachment most likely lay on the sea floor, and seem to have expanded their diameter more rapidly and have more septa.

There are a number of species recognized in Europe that resemble *M. concinnula*. These are species such as *M. carnockii* Rozkowska (1953, p. 24), with short, heavily dilated septa, few internal dissepiments and a broad, open tabularium, or those with a small diameter and cylindrical external form.

Occurrence.—This species occurs only within the top beds of the lower biostrome of the Nora Member of the Shell Rock Formation, and is most abundant within this unit north of Nora Springs, in what Belanski termed the "Reed Creek Phase" (1927, p. 359), which is the Reed Creek Locality (Locality 4, Appendix). The holotype was collected at the same level a bit farther north at the Bjorgeson locality of Belanski (Locality 3, Appendix).

Etymology.—This name was on a label in the Belanski collection, without explanation.

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APPENDIX—FOSSIL LOCALITIES

SHELL ROCK FORMATION

Nora Springs, Iowa, 7.5' Quadrangle

1. Quarry North of Keidle's Bluff. C, NE $\frac{1}{4}$, SW $\frac{1}{4}$, Sec. 26, T.97N., R.19W., Cerro Gordo Co.; 0.3 km (0.2 mi) due north of Keidle's Bluff on Shell Rock River. Nora and Rock Grove Members of Shell Rock Fm. lie unconformably on lower Cedar Valley units.

2. Weitsie's Bluffs. Along Shell Rock River; Weitsie's Bluff locality of Belanski; W $\frac{1}{2}$, NE $\frac{1}{4}$, Sec. 35, T.97N., R.19W., Cerro Gordo Co., Conservation Park on east side of Shell Rock River. Nora Member limestones lie directly on lower Cedar Valley dolomitic sequence.

3. Bjorgason. Series of low outcrops along Shell Rock River, Bjorgason "Phase" of Belanski (1927, p. 361), SE $\frac{1}{4}$, SE $\frac{1}{4}$, Sec. 35, T.97N., R.19W., Cerro Gordo Co., on west side of Shell Rock River. Nora and Rock Grove Members occur above brown dolomites of underlying unit of Cedar Valley.

4. Reed Creek. Low cliff of very fossiliferous limestones on west side of Shell Rock River, "Reed Creek Phase" of Belanski (1927, p. 359); C, SE $\frac{1}{4}$, NW $\frac{1}{4}$, Sec. 1, T.96N., R.19W., Cerro Gordo Co. Lower Nora biostrome exposed along river bank with great multitude of corals present. Approximately 300 m northeast of riverside outcrop is section 4a, just down slope from fork in county road, presently poorly exposed but a clean outcrop in 1970 with both biostromes of Nora Member well exposed, along with overlying Juniper Hill Shale.

5. South Reed Creek. C west line, SE $\frac{1}{4}$, Sec. 1, T.96N., R.19W., Cerro Gordo Co., east bank of Shell Rock River, in wooded bluffs along river with both lower and upper biostromes of the Nora Member exposed from slightly above river level to bluffs, and approximately 0.8 m of Rock Grove dolomites exposed at river level.

6. North Nora Springs. NE corner, SE $\frac{1}{4}$, NE $\frac{1}{4}$, Sec. 12, T.96N., R.19W., Cerro Gordo Co., east bank of Shell Rock River, in banks along river. Both lower and upper biostromes of Nora Member exposed in bluffs above river.

7. North line, SW $\frac{1}{4}$, Sec. 7, T.96N., R.18W., Floyd Co., on south (western) bank of Shell Rock River, in north-facing banks of river. In 1968, exposures of both Nora biostromes as well as underlying yellow brown dolomites of Rock Grove Member were present, since greatly obscured by grading and slumping.

8. Nora Dam. Center, Sec. 7., T.96N., R.18W.,

Floyd Co., on northwest edge of Nora Springs, with 1.3 to 1.7 m of uppermost Mason City Member limestones normally exposed below dam (old mill dam, with abandoned millrace north of present channel).

9. Nora Springs. Eastern $\frac{1}{2}$, SE $\frac{1}{4}$, Sec. 7, T.96N., R.18W., Floyd Co., cliffs on east bank of Shell Rock River in Nora Springs, Iowa. This is the type locality of the Mason City Member of the Shell Rock Formation. Total Mason City outcrops for 0.4 to 0.6 km (0.25 to 0.37 mi) on each side of, and under, highway bridge of U.S. 18, on west side of Nora Springs.

10. South Nora Springs. NE corner, SE $\frac{1}{4}$, Sec. 18, and NW $\frac{1}{4}$, NW $\frac{1}{4}$, Sec. 17, T.96N., R.18W., Floyd Co., cliffs on south (right) bank of Shell Rock River, exposures of the Mason City Member, with faunas difficult to collect because of steepness of outcrop and weathering rind on north-facing cliff.

Rudd, Iowa, 7.5' Quadrangle

11. Reference Section. N $\frac{1}{2}$, NE $\frac{1}{4}$, NE $\frac{1}{4}$, Sec. 17, T.96N., R.18W., Floyd Co., abandoned quarry on what was the Sherman Buffalo Farm in 1968, largely overgrown in 1986, but adopted as reference section for Nora and Rock Grove Members by Koch (1970, p. 67).

12. Rudd. NW $\frac{1}{4}$, SE $\frac{1}{4}$, Sec. 13, T.96N., R.18W., Floyd Co., abandoned quarry and small outcrops along Flood Creek, 190 m north of railroad trestle over creek on west side of Rudd, Iowa. Clean exposures of both lower and upper Nora biostromes were available 1967–1970, but considerably overgrown and dumped on by 1986. Also, there is a small outcrop of lower Nora biostrome on west side of Flood Creek 50 m south of railroad trestle.

Mason City SE, Iowa, 7.5' Quadrangle

13. McEachron Quarry. SW $\frac{1}{4}$, SW $\frac{1}{4}$, NW $\frac{1}{4}$, Sec. 20, T.96N., R.19W., Cerro Gordo Co., abandoned quarry previously known as McEachran Quarry (Koch, 1970, p. 88), on east side of county road 0.8 km (0.5 mi) south of Portland, Iowa, and on south side of the Winnebago River. Nora biostrome lies unconformably on lower Cedar Valley.

14. County Roads Quarry. NE corner, SE $\frac{1}{4}$, SE $\frac{1}{4}$, Sec. 36, T.96N., R.19W., Cerro Gordo Co., located between forked roads just south of Winnebago River. Upper biostrome of Nora Member is exposed around 1–1.5 acre flooded quarry.

Rockford, Iowa, 7.5' Quadrangle

15. Old Rock Grove Mill. SE $\frac{1}{4}$, SW $\frac{1}{4}$, NE $\frac{1}{4}$, Sec. 20, T.96N., R.18W., Floyd Co., on east (left) bank of Shell Rock River, on north side of county road, below old foundation of Rock Grove Mill, 0.2 km (0.1 mi)

SW of Rock Grove Cemetery. Approximately 2.9 m of Mason City beds overly lower Cedar Valley and are overlain by lower Rock Grove Member dolomites.

16. Tom Williams Quarry. SW $\frac{1}{4}$, SW $\frac{1}{4}$, Sec. 28, T.96N., R.18W., Floyd Co., large quarry presently (1986) being extended to occupy most of east half of approximately 20 acre tract on east side of Shell Rock River. This was operated (1986) as the Greene Bros. Quarry, but had been known for years as the Tom Williams Quarry (Koch, 1970, p. 71). The lower biostrome of the Nora, all of the Rock Grove and virtually all of the Mason City Member are exposed at this locality.

17. Baumgardner's Mill. C, SW $\frac{1}{4}$, SW $\frac{1}{4}$, Sec. 28, T.96N., R.18W., Floyd Co. on east (left) bank of Shell Rock River, along what was formerly the millrace of Baumgardner's Mill, site of the "Baumgardner's Phase" of Belanski (1927, p. 394) and Koch (1970, p. 73). This was a classic outcrop of the entire Mason City Member and much of the overlying Rock Grove Member. In 1986 this was in process of being covered over by stripping of quarry area to the east, with soil bulldozed into the millrace.

18. Kapka's Farm. S $\frac{1}{2}$, NE $\frac{1}{4}$, NW $\frac{1}{4}$, Sec. 4, T. 95N., R.18W., Floyd Co. on south (right) bank of Shell Rock River, low wooded cliffs on what was formerly Kapka's Farm (1970). This is locality 155 of Belanski (Strimple and Leverson, 1969, p. 270), approximately 2.4 km (1.5 mi) northwest of Rockford. Here 3 m of Mason City beds are exposed above the summer river level.

19. Cooper's Bend. South line, SW $\frac{1}{4}$, SE $\frac{1}{4}$, Sec. 33, T.96N., R.18W., Floyd County, on northeast (left) bank of Shell Rock River, and Cooper's Bend locality of Belanski, with low cliffs of Mason City Member limestones in wooded section of shore.

20. West Rockford. SW $\frac{1}{4}$, NE $\frac{1}{4}$, NW $\frac{1}{4}$, Sec. 15, T.95N., R.18W., Floyd County, on north (left) bank of Winnebago River, immediately west of abandoned bridge abutment on south side of Rockford, 33 m west of new county highway bridge. Complete section of Nora Member is exposed, along with upper 1–1.1 m of Rock Grove Member. This is the "Rockford Phase" of Belanski (1927, p. 352) and the Rockford section of Koch (1970, p. 74).

21. South of Rockford. Bulldozed and stripped area on west side of county road adjacent to (1967) bridge over the Shell Rock River approximately 5.6 km (3.5 mi) south of Rockford in the NE Corner, SE $\frac{1}{4}$, NE $\frac{1}{4}$, Sec. 35, T. 95 N., R. 18 W. These were temporary exposures of the Upper Nora biostrome, with very abundant fauna at the base, overlying yellow Rock Grove dolomites.

Roseville, Iowa, 7.5' Quadrangle

22. Roseville. SW corner, SE $\frac{1}{4}$, Sec. 25, T.95N., R.17W., Floyd County, on north side of county road. Low outcrop of approximately 1.6 m of Mason City Member overlying lower Cedar Valley unit. This is the Roseville "Phase" of Belanski (1927, p. 356) and the Roseville outcrop of Koch (1970, p. 75). It was well exposed in 1967 and 1968 but largely covered by 1986.

23. Marble Rock Quarry. Abandoned quarry on the north side (left bank) of Shell Rock River approximately 1.6 km (1 mi) upstream of Marble Rock, Iowa. Quarry is in SE $\frac{1}{4}$, NW $\frac{1}{4}$, Sec. 8, T.94N., R.17W., where complete section of Mason City limestones overly lower Cedar Valley unit. Marble Rock "Phase" of Belanski (1927, p. 354).

24. Maxson Quarry. Active (1986) quarry in SE $\frac{1}{4}$, SE $\frac{1}{4}$, Sec. 7, T.94N., R.17W., Floyd County, slightly more than 1.6 km (1 mi) west of Marble Rock, on south (right) shore of Shell Rock River. This section has been described by Bunker, Witzke and Day (1986, p. 41). Approximately 3.8 m of the Mason City beds are exposed above the Lithograph City Formation, placed in the Cedar Valley Group by these authors.

LIME CREEK FORMATION Hanford, Iowa, 7.5' Quadrangle

25. Owen Grove West. North banks of Big Gully in pasture occupying NE $\frac{1}{4}$, SE $\frac{1}{4}$, Sec. 36, T.96N., R.20W., Cerro Gordo County, Iowa, and along Owen Creek. Outcrops of *Acervularia* beds of Owen Member outcrop sporadically in pasture. This is at the west edge of what was once commonly known as Owen Grove.

26. Owen Grove. In Owen Grove itself, best exposed are the *Acervularia* beds in abandoned quarry in NE $\frac{1}{4}$, SW $\frac{1}{4}$, SW $\frac{1}{4}$ Sec. 31, T.96N., R.19W., Cerro Gordo County, Iowa. Outcrops also are present along south bank of Owen Creek in Big Gully, in SW $\frac{1}{4}$, NE $\frac{1}{4}$, SW $\frac{1}{4}$ of Sec. 31, but are of lower rocks of Owen Member. Rocks of upper Cerro Gordo Member are exposed in north bank of creek at approximate center of Sec. 31.

Mason City SE, Iowa, 7.5' Quadrangle

27. South Portland. Outcrops on both north and south sides of county road, with exposures along drainage ditches (which were clear and fresh in 1967 & 1968, but largely covered over by 1986) along boundary line in NE corner, NE $\frac{1}{4}$, Sec. 31, T. 96N., R.19W., in Cerro Gordo County, Iowa. The upper part of the Cerro Gordo Member, the "*Spirifer*" beds of Fenton and Fenton was completely exposed in 1967, along with the upper part of their "*striatula* zone".

27a. In roadside exposures 0.5 km (0.33 mi) south of locality 27 could be seen outcrops of the same "*Spirifer* zone" of the Cerro Gordo Member, including the same rusty bed with colonial corals at the base of the "*Spirifer* zone", above the plastic clay of the "*Douvillina* zone". Outcrops were along the west side of the paved road, 4 km (2.6 mi) due south of Portland, in the SE corner, SE $\frac{1}{4}$, NE $\frac{1}{4}$, Sec. 31, T.96N., R.19W., Cerro Gordo County.

28. Type Lime Creek. The "Claybanks" County Conservation Park, bluffs on south (right) bank of the Winnebago River, 4.8 km (3 mi) downstream from Portland, Iowa. This is the type locality of the Hackberry Stage of Webster (1887), and of the Lime Creek Formation (Calvin, 1897). The river called Lime Creek in Calvin's time had a name change to Winnebago River prior to the 1920's. The type locality is located in the NE $\frac{1}{4}$, SE $\frac{1}{4}$, NE $\frac{1}{4}$ of Sec. 34, and extends into the SW $\frac{1}{4}$, NW $\frac{1}{4}$, Sec. 35., T.96N., R.19W. The outcrop was fairly clean and 70% exposed in 1968, but presently is largely matted over with mud. This area is an eastward extension of the wooded area previously known locally as Hackberry Grove. Lime Creek beds exposed here in 1970 ranged from the Juniper Hill Member at and above river level, extending up through the entire Cerro Gordo Member, to the basal part of the Owen Member, exposed high in a southward-trending gully south of the "claybanks" in the SE $\frac{1}{4}$ of the NE $\frac{1}{4}$ of section 34.

28a. West Hackberry Grove. Approximately 0.6 Km (0.4 mi.) west of the type Lime Creek section in Claybanks Conservation Park, these poor outcrops of the Cerro Gordo Member with float from the Owen occur in the SW $\frac{1}{4}$, NE $\frac{1}{4}$, Sec. 34, T.96N., R.19W., along the east face of a southward trending gully tributary to the Winnebago River.

28b. Lime Creek East. East and southeast of the type section of the Lime Creek Formation, two plowed fields have yielded abundant colonial corals from the "*Spirifer*" beds of the Cerro Gordo Member. The more northwesterly situated field is in the NW $\frac{1}{4}$, SE $\frac{1}{4}$, NW $\frac{1}{4}$, Sec. 35, and the more easterly one in the NE corner, NW $\frac{1}{4}$, SE $\frac{1}{4}$, Sec. 35, T.96N., R.19W. In both fields plowing brings abundant corals to the surface each spring.

29. County Line Road North. Outcrops along North-South county road situated on the Cerro Gordo-Floyd County line, along the east line of the SE $\frac{1}{4}$, NE $\frac{1}{4}$, Sec. 1, T.95N., R.19W., are of the Cerro Gordo Member of the Lime Creek, with the basal bed of the Owen Member exposed at the summit of the north facing hill, the escarpment of the Cerro Gordo and Owen Members. The roadside ditches, freshly cleaned out and highly fossiliferous in 1968 and 1970 were

much overgrown and apparently devoid of fossils in 1986.

30. Bird Hill North. Situated 2 km (1.3 mi) due south of Locality 29 are low exposures of the Cerro Gordo Member, situated in roadside ditches, along the east line of NE $\frac{1}{4}$, SE $\frac{1}{4}$, Sec. 12, relatively clean and richly fossiliferous in 1968 and 1970, but overgrown and relatively unfossiliferous in 1986. These low outcrops, along with those at nearby Bird Hill were formerly the richest known for solitary corals of the "*Spirifer*" beds of the Cerro Gordo.

31. Bird Hill. One of the most famous of the Iowa Devonian collecting localities, situated on the east-west county road forming the south line of the SE $\frac{1}{4}$ of Section 13, T.95N., R.19W. Cerro Gordo County, where straightening of the road led to cutting away of a bank of extremely fossiliferous Cerro Gordo beds. These have been heavily tramped and collected for the past 40 years or more, and in 1986 were largely covered and overgrown, with fewer fossils available. This was the locality with most abundant rugose corals in the unit.

32. Bird Hill South. Along north-south road running up Cerro Gordo escarpment 0.6 km (0.4 mi) southeast of locality 31, along center of east line, NE $\frac{1}{4}$, Sec. 24, T.95N., R.19W. Cerro Gordo County. This formerly was an abundantly fossiliferous and relatively clean section of the Cerro Gordo Member, but in 1986 was considerably grassed over.

33. Bird Hill East. Roadside outcrop of Cerro Gordo beds 1.6 km (1 mi) ESE of locality 32 along E line, SE $\frac{1}{4}$, NE $\frac{1}{4}$, Sec. 19, T.95N., R.18W., Floyd County.

Rockford, Iowa, 7.5' Quadrangle

34. Juniper Hill. NW corner, NE $\frac{1}{4}$, Sec. 17, T.95N., R.18W., Floyd County, with sporadic natural outcrops of the Cerro Gordo Member.

35. Rockford Brick and Tile Co. Quarry. In disuse in 1986, located in S $\frac{1}{2}$, NW $\frac{1}{4}$, Sec. 16, T.95N., R.18W., Floyd County, on north side of paved east-west road southwest of Rockford, Iowa. This is justifiably the most famous Upper Devonian fossil locality in Iowa. The quarry which formerly had extensive stripped surfaces and freshly quarried faces provided renewed collecting areas each year, and hundreds of thousands of superb fossils were disseminated to collections throughout the world. The Brick and Tile Company is no longer in operation since the early

1980's and the quality of outcrops has declined greatly and collecting pressure has greatly lessened the availability of fossil faunas. The quarry formerly exposed a superb section of virtually all of the Juniper Hill and Cerro Gordo Members.

Sheffield, Iowa, 7.5' Quadrangle

36. West Rockwell. Formerly exposed were beds of most of the Owen Member, in an abandoned Quarry, now utilized as a dump by the town and in the process of being filled in; quarry situated in SW $\frac{1}{4}$, NW $\frac{1}{4}$, SW $\frac{1}{4}$, Sec. 3, T.94N., R.20W., Cerro Gordo County, situated on east side of north-south U.S. Highway 65.

37. Linn Grove. Town park in Rockwell, where an old quarry in Linn Grove provides some overgrown outcrops of the Owen Member in NE $\frac{1}{4}$, NW $\frac{1}{4}$, Sec. 10, T.94N., R.20W., Cerro Gordo County.

38. Lillibridge Quarry. Excellent and extensive exposures of the complete Owen Member in large quarry occupying most of the E $\frac{1}{2}$, SW $\frac{1}{4}$, Sec. 26, T.94N., R.20W., Cerro Gordo County, 5.6 km (3.5 mi) south and 1.6 km (1 mi) east of Rockwell, Iowa.

Hansell, Iowa, 7.5' Quadrangle

39. Morgan Quarry. 3.2 km (2 mi) west and 2.5 km (1.5 mi) south of Aredale, Iowa, in SW $\frac{1}{4}$, NW $\frac{1}{4}$, Sec. 1, T.92N., R.19W., Franklin County. This quarry, in 1986 partly overgrown, formerly provided excellent exposures of the lower $\frac{2}{3}$ of the Owen Member.

Dumont South, Iowa, 7.5' Quadrangle

40. Buseman Quarry. Formerly operated by Greene Brothers, 7.6 km (4.8 mi) due south of Dumont, Iowa, on the west side of county highway in SE $\frac{1}{4}$, SE $\frac{1}{4}$, Sec. 21, T.91N., R.18W., Butler County. This quarry formerly exposed a complete section of the Owen Member beds, but in 1986 was no longer active and was partially filled with water. A clean sequence of much of the Owen is still exposed here.

40A. North Buseman Quarry. Abandoned quarry 0.2 km (0.12 mi) north of the Buseman Quarry, where beds of the Owen Member were exposed.

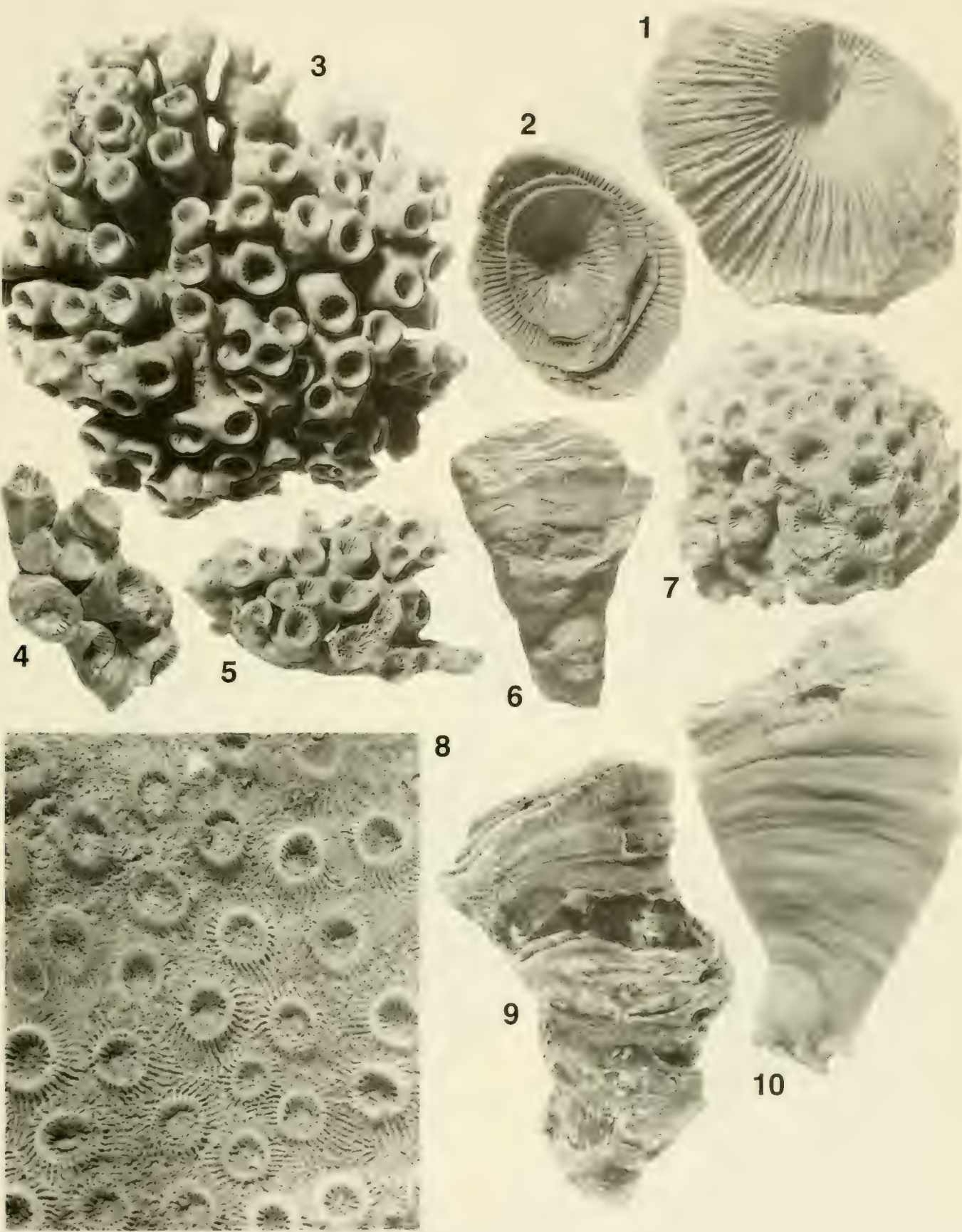
41. Carrolus Quarry. Flooded in 1986. When active, exposed a complete sequence of the Owen Member beds, features good exposures above the water line in the SE $\frac{1}{4}$, SE $\frac{1}{4}$, Sec. 34, T.91N., R.18W., Butler County, 11.3 km (7 mi) south and 1.6 km (1 mi) E. of Dumont, Iowa.

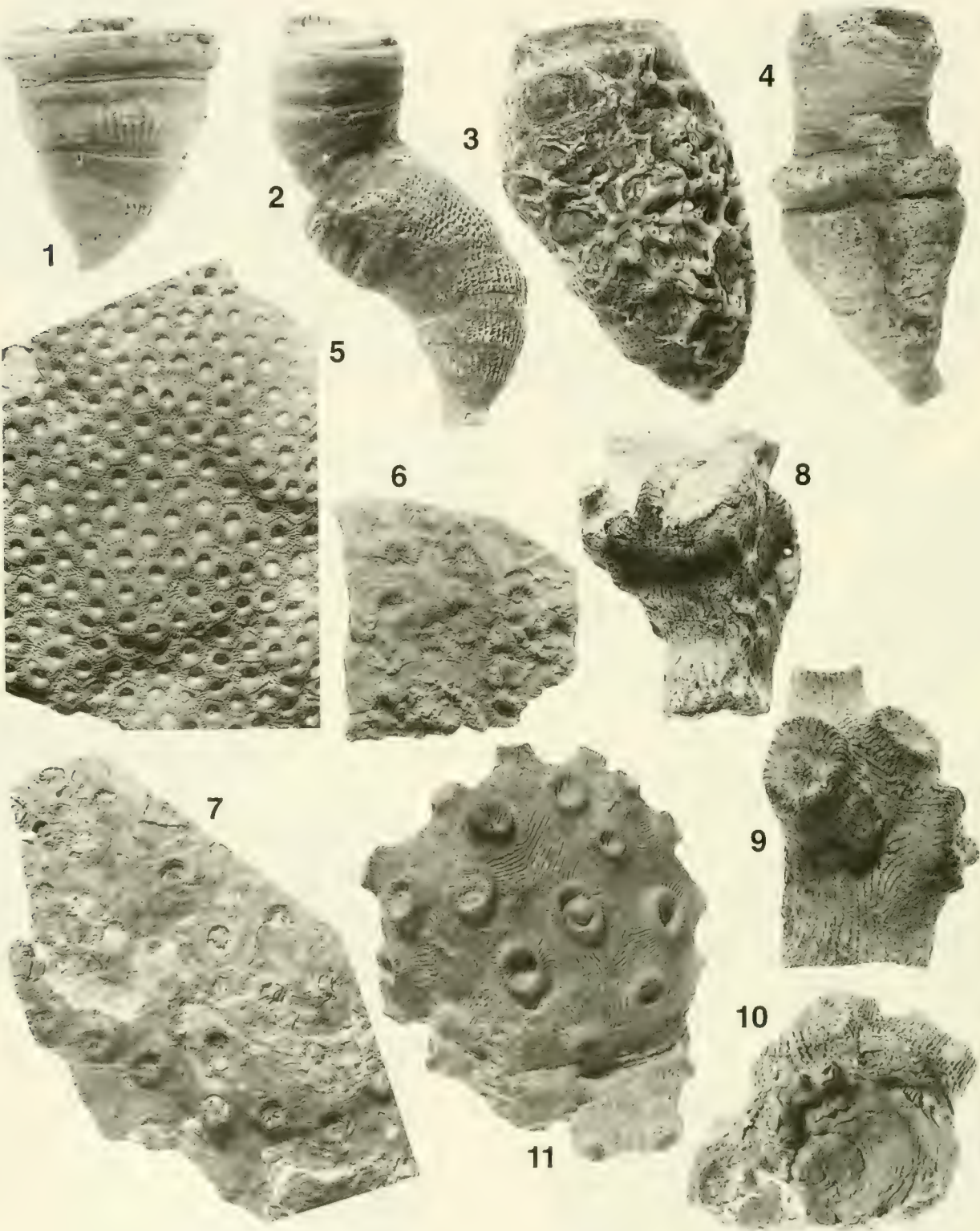
EXPLANATION OF PLATE I

Figure

1-10. External Views. Frasnian Corals from Iowa

1. *Tabulophyllum curtum* n. sp., holotype, S.U.I. 858, Belanski Coll., (Same as Plate 14, figs. 10,11), $\times$ 1. Uppermost Mason City Member.
2. *Tabulophyllum* n. sp. A., S.U.I. 643, Belanski Coll., Lower biostrome, Nora Member, $\times$ 1.
3. *Disphyllum floydense* (Belanski), paratype, S.U.I. 2003 Belanski Coll., Uppermost Mason City Member, $\times$ 1.
4. *Disphyllum iowensis* n. sp., holotype, S.U.I. 213, Belanski Coll., Lower unit, Mason City Member, $\times$ 1.
5. *Disphyllum conjugans* Belanski, paratype, S.U.I. 1376, Belanski Coll., Uppermost Mason City Member, $\times$ 1.
6. *Tabulophyllum mutabile* n. sp., S.U.I. 1266, Belanski Coll., Middle unit, Mason City Member. (Baumgardner's Mill, Locality 17, Appendix), $\times$ 1.
7. *Hexagonaria oweni* (Belanski), S.U.I. 471, Belanski Coll., holotype, Upper biostrome, Nora Member, (Rudd, Locality 12, Appendix), $\times$ 1.
8. *Pachyphyllum gregarium*, P.R.I. 44785, Upper biostrome, Nora Member, (South of Rockford, Locality 21, Appendix), $\times$ 1.
9. *Tabulophyllum rectum* Fenton and Fenton, P.R.I. 44701, Upper Cerro Gordo Member, (North of Bird Hill, Locality 30, collected by Calvin Levorson). $\times$ 2.
10. *Tabulophyllum ehlersi* Fenton and Fenton, P.R.I. 44702, Upper Cerro Gordo Member, (North of Bird Hill, Locality 30, collected by Calvin Levorson). $\times$ 2.





EXPLANATION OF PLATE 2

Figure

1-11. External view of Frasnian corals of Iowa

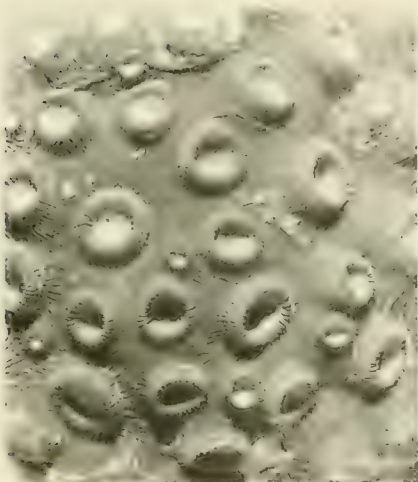
- 1-4. *Characterophyllum nanum* (Hall and Whitfield, 1873), upper Cerro Gordo Member, Lime Creek Fm., all from North of Bird Hill, Locality 30, collected by Calvin Levorson, all $\times 2$. 1. P.R.I. 44735, 2. P.R.I. 44736, 3. P.R.I. 44737, 4. P.R.I. 44738.
5. *Hexagonaria inequalis* (Hall and Whitfield, 1873), paratype, F.M.N.H. 26055 (same specimen as Plate 35, Figure 2), $\times 1$. Upper Cerro Gordo Member, (Type Lime Creek Fm., Section 28, Appendix).
6. *Iowaphyllum johanni* (Hall and Whitfield, 1873), F.M.N.H. 25772, (Same specimen as Plate 4, Figure 4), $\times 1$. Upper Cerro Gordo Member, Lime Creek Formation, (Type Lime Creek Fm., Locality 28, Appendix).
7. *Iowaphyllum johanni* (Hall and Whitfield, 1873), F.M.N.H. 26053, (holotype of *Strombodes marginatus* Fenton and Fenton, 1924, illustrated by Fenton and Fenton, 1924, Plate XV, Figure 5), $\times 1$. Upper Cerro Gordo Member, (Type Lime Creek Fm., Locality 28, Appendix).
- 8-11. *Pachyphyllum woodmani* (Hall and Whitfield, 1873). 8. P.R.I. 44795, Upper Cerro Gordo Member, $\times 2$. Base was on a brachiopod shell, with a very long founding corallite prior to typical budding. 9. P.R.I. 44796, $\times 2$. 10. P.R.I. 44797, $\times 2$. 11. P.R.I. 44798, $\times 1$. All are from the former Rockford Brick and Tile Co. quarry, Rockford, Iowa (Locality 35, Appendix).

EXPLANATION OF PLATE 3

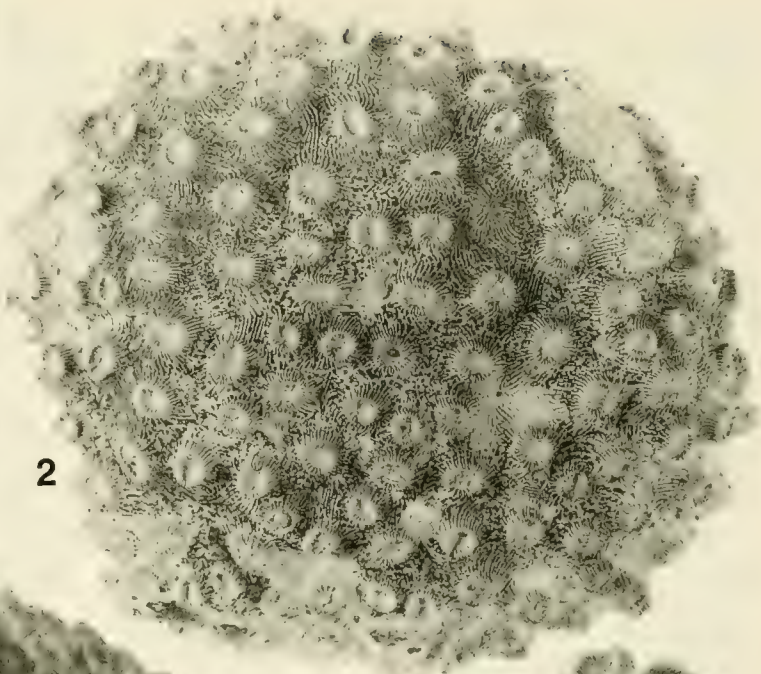
Figure

1-7. External views of Frasnian corals of Iowa

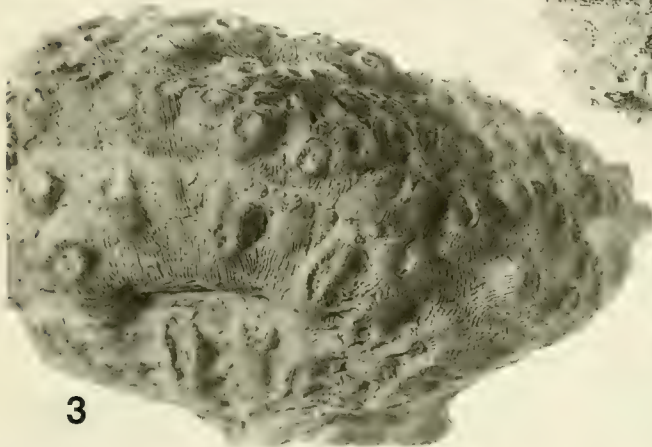
1. *Pachyphyllum woodmani*, F.M.N.H. 26017 (same as external view in Fenton and Fenton, Plate 8, Figure 2, of "Plesiotype"), Upper Cerro Gordo Member, (Type Lime Creek Fm., Locality 28, Appendix), $\times 1$.
- 2-4. *Pachyphyllum woodmani*, Upper Cerro Gordo Member, (Former Rockford Brick and Tile Company Quarry, Locality 35, Appendix), all $\times 1$. 2. P.R.I. 44799, 3. P.R.I. 44800, 4. P.R.I. 44801.
5. *Pachyphyllum crassicostatum* Webster 1889, F.M.N.H. 26030, ("Plesiotype" of Fenton and Fenton, 1924), Uppermost Owen Member, (Type Owen, Locality 26, Appendix), $\times 1$.
6. *Pachyphyllum crassicostatum* Webster 1889, S.U.I. 3057, Belanski Coll., Uppermost Owen Member (West Hackberry Grove, Locality 28A, Appendix), $\times 1$.
7. *Hexagonaria bassleri*, P.R.I. 44765, Uppermost Owen Member, (Lillibridge Quarry, Locality 38, Appendix), $\times 2$.



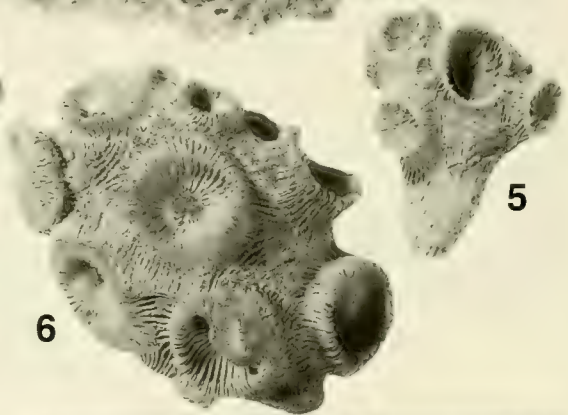
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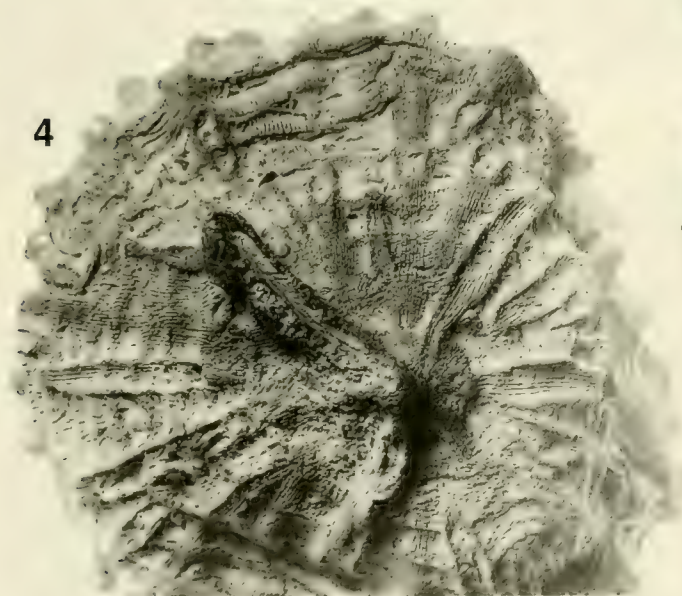


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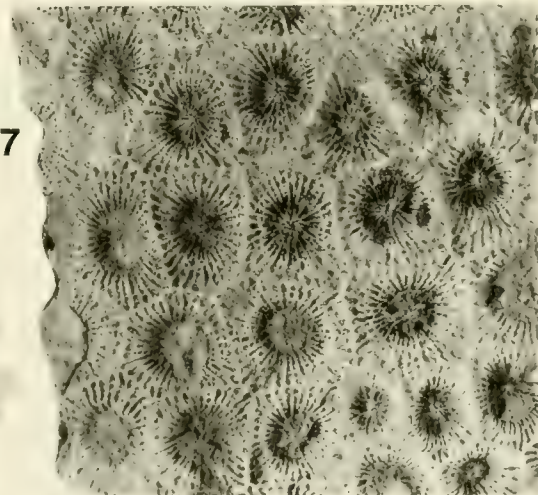


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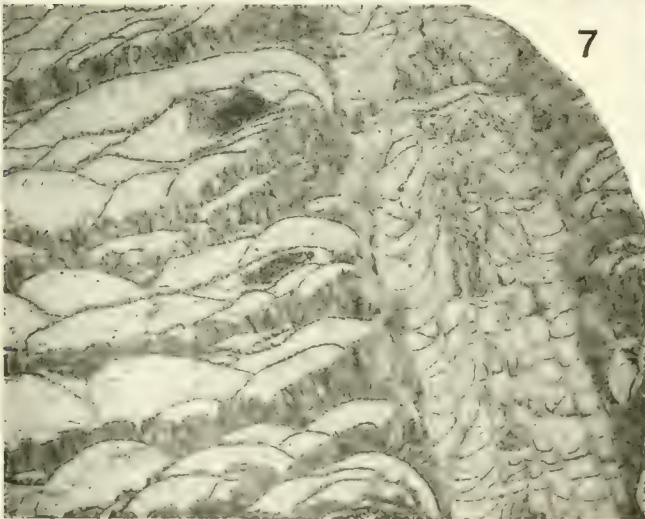
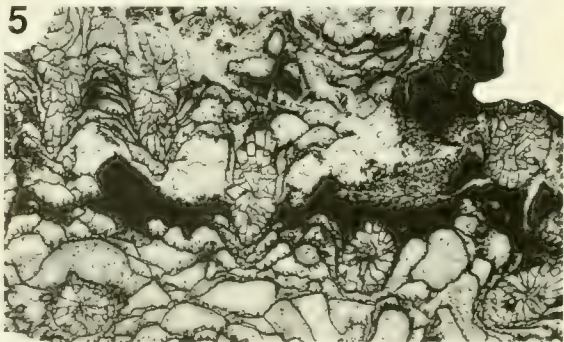
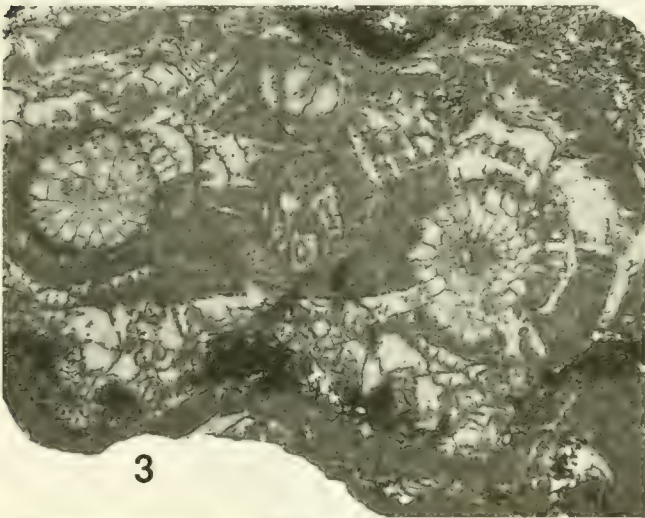
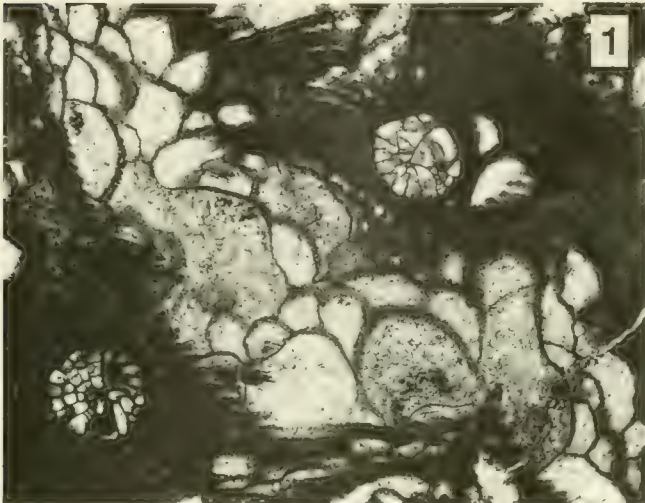
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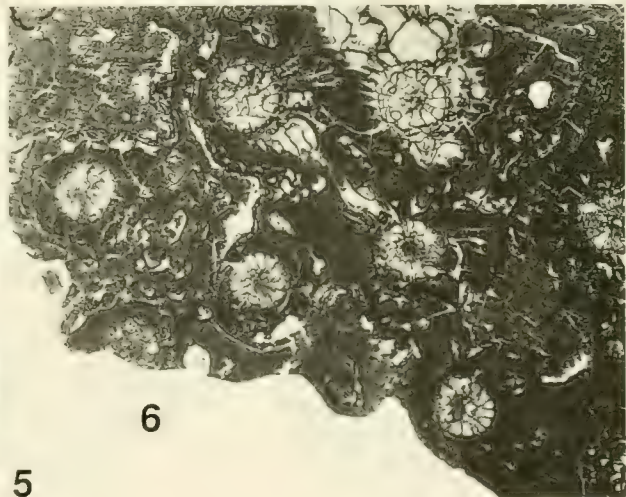
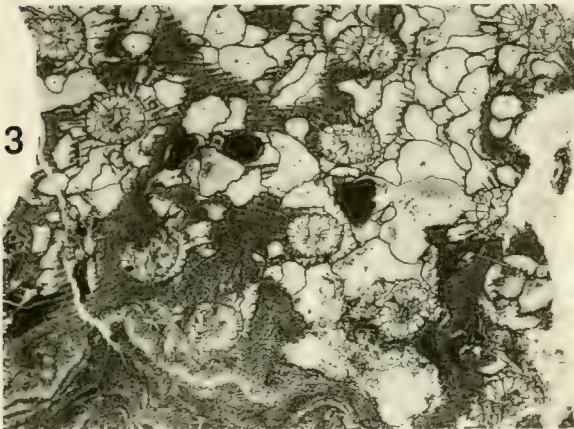


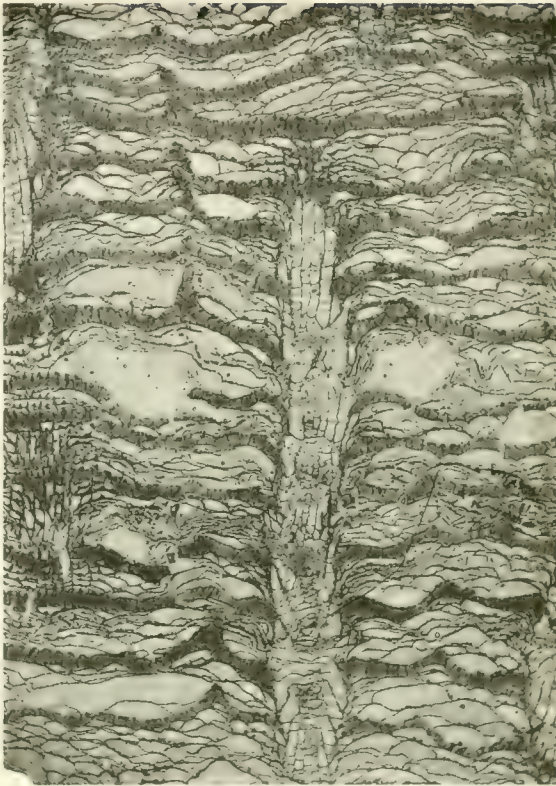
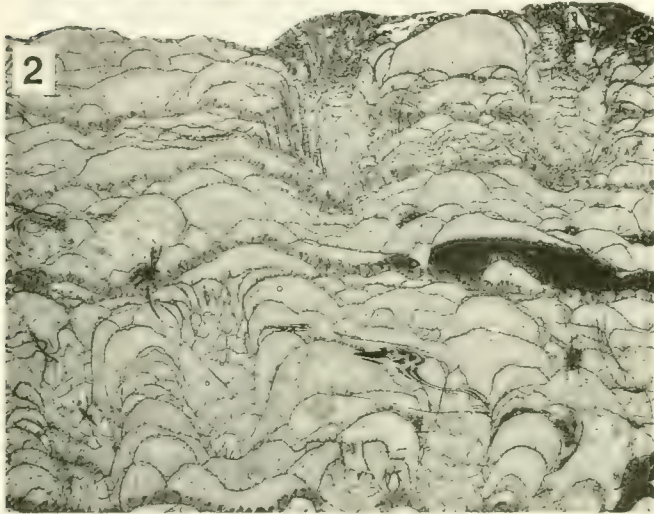
EXPLANATION OF PLATE 4

Figure	Page
1-7. <i>Iowaphyllum johanni</i> (Hall and Whitfield, 1873)	31
1, 2. N.Y.S.M. 3720/1, holotype, 1. transverse of corallites with heavy septal crusts and large, irregular dissepiments, $\times 5$; 2. longitudinal with heavy septal crusts around tabularium, $\times 5$.	
3. N.Y.S.M. 3721/1, transverse of holotype of <i>Smithia multiradiata</i> with large corallites and widespread septal crusts and crests, $\times 5$.	
4. F.M.N.H. 25772, transverse, specimen with light crusts and huge dissepiments, $\times 2$.	
5. F.M.N.H. 26053, holotype of <i>Strombodes marginatus</i> , transverse, illustrating large dissepiments, $\times 2$.	
6, 7. U.M.M.P. 8087, Paratype of <i>Strombodes marginatus</i> . 6. transverse, showing septal crests and very large dissepiments, $\times 2$; 7. longitudinal of trabecular crusts thickest close to tabularium, $\times 6$.	

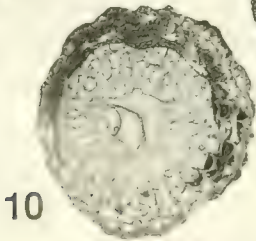
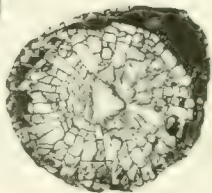
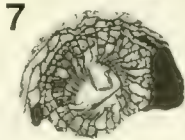
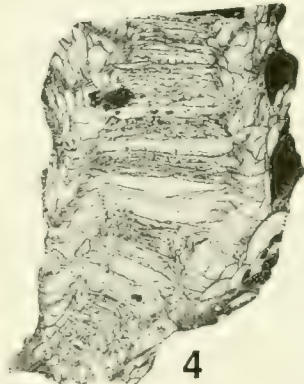
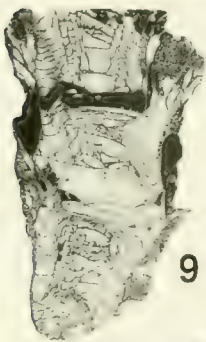
EXPLANATION OF PLATE 5

Figure	Page
1-6. <i>Iowaphyllum johanni</i> (Hall and Whitfield, 1873)	31
1. U.M.M.P. 8087, paratype of <i>Strombodes marginatus</i> , transverse enlarged to illustrate septal crests, $\times 5$.	
2. P.R.I. 44692, transverse of colony with septal crests and "walls", $\times 2$.	
3. P.R.I. 44693, transverse, with crests and large dissepiments, $\times 2$.	
4. P.R.I. 44694, transverse of specimen with very large dissepiments, $\times 2$.	
5. P.R.I. 44695, transverse, showing extremely large, irregular dissepiments, $\times 2$.	
6. P.R.I. 44696, transverse, with very widespread crusts, $\times 2$.	





3

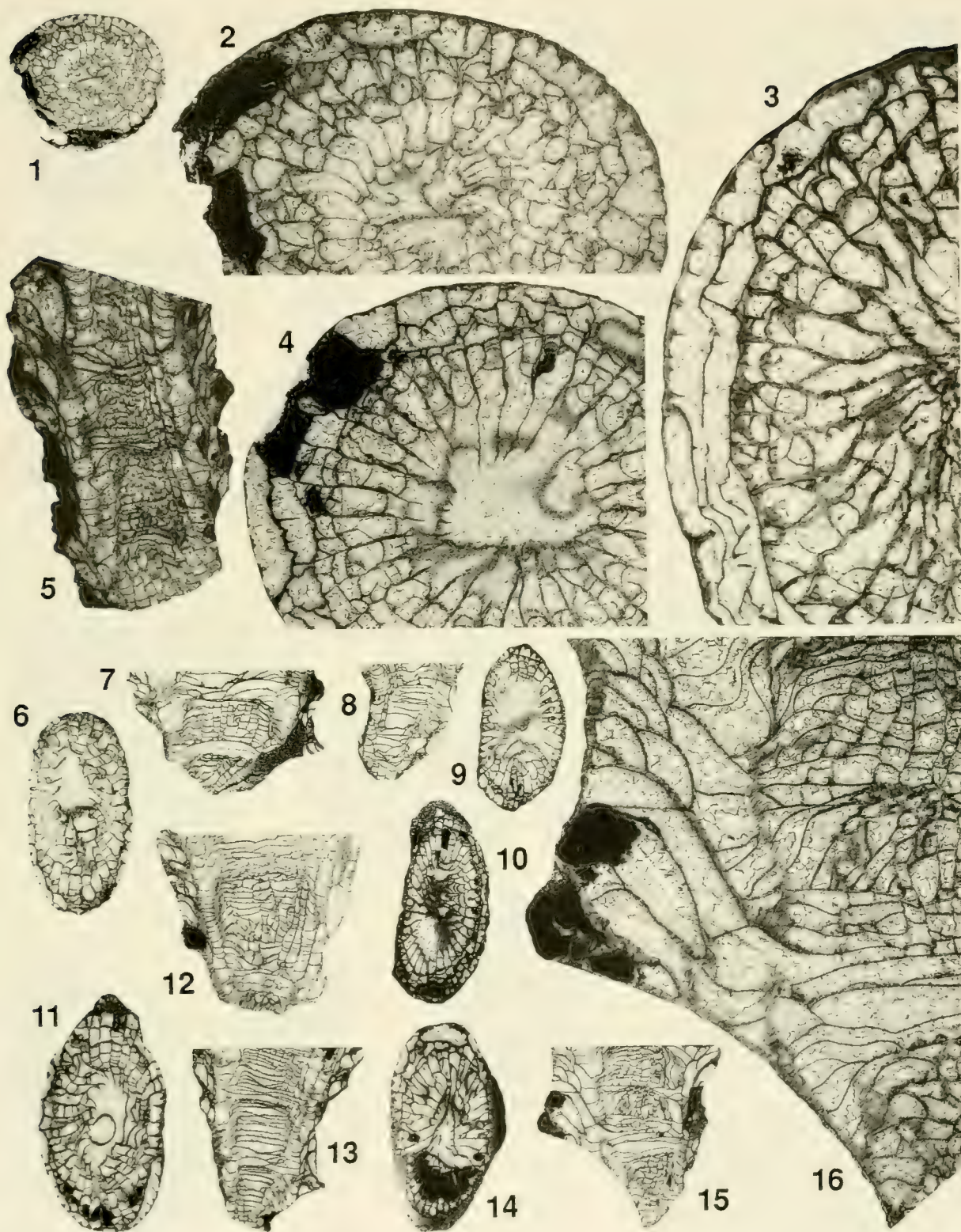


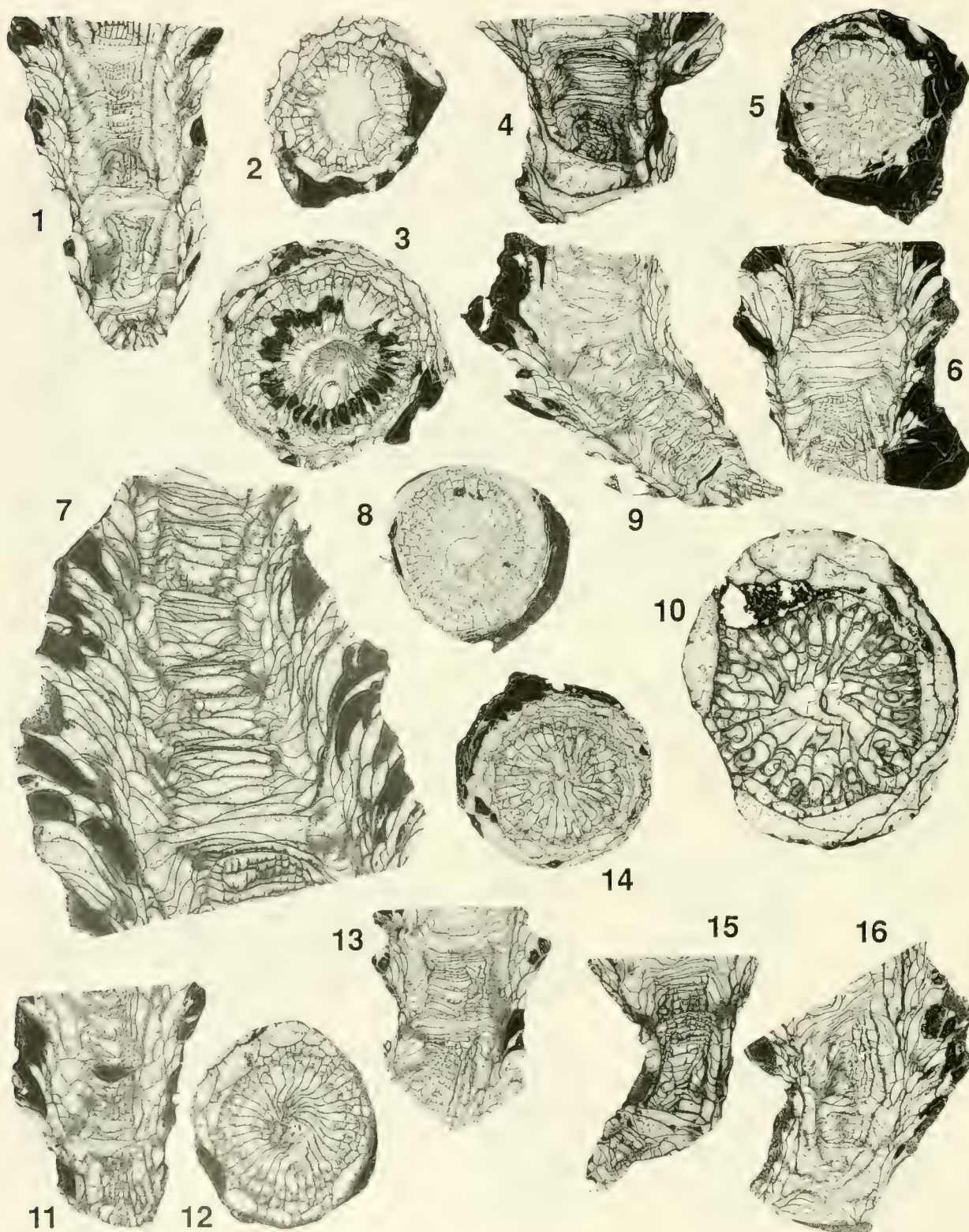
EXPLANATION OF PLATE 6

Figure	Page
1-3. <i>Iowaphyllum johanni</i> (Hall and Whitfield, 1873)	31
1. P.R.I. 44696, longitudinal, with septal crusts separated by large, uniform dissepiments, $\times 6$.	
2. P.R.I. 44692, longitudinal of colony with extremely irregular dissepiments, $\times 2.5$.	
3. P.R.I. 44694, longitudinal to show periodic development of crusts with "walls" separating corallites, $\times 2.5$.	
4-10. <i>Tabulophyllum rectum</i> Fenton and Fenton, 1924	34
4, 5. U.M.M.P. 7834, holotype, 4. longitudinal with flat-topped tabulae and presepiments preferentially developed on right side, $\times 2$; 5. transverse, with small lonsdaleoid dissepimentarium, $\times 2$.	
6, 7. U.M.M.P. 7835, 6. longitudinal of paratype with regular tabulae, $\times 2$; 7. transverse, $\times 2$.	
8. U.M.M.P. 7836, longitudinal of paratype with amplexoid septa and preferential development of presepiments on convex side of corallite, $\times 2$.	
9, 10. F.M.N.H. 26006, holotype of <i>T. erraticum</i> , 9. longitudinal of marked expansions and contractions of dissepimentarium, $\times 2$; 10. transverse, $\times 2$.	

EXPLANATION OF PLATE 7

Figure	Page
1-5. <i>Tabulophyllum rectum</i> Fenton and Fenton, 1924	34
1, 2. P.R.I. 44697, 1. transverse, $\times 2$; 2. enlarged view of characteristic dissepimentarium, $\times 6$.	
3. P.R.I. 44698, transverse, illustrating typical "wall" on innermost presepiments, $\times 8$.	
4. P.R.I. 44699, transverse, $\times 5$.	
5. P.R.I. 44700, longitudinal, $\times 2$.	
6-16. <i>Tabulophyllum ehlersi</i> Fenton and Fenton, 1924	35
6, 7. U.M.M.P. 7815, holotype, 6. transverse, $\times 2$; longitudinal, $\times 2$.	
8, 9. U.M.M.P. 7818, paratype, 8. longitudinal, $\times 2$; 9. transverse, $\times 2$.	
10. U.M.M.P. 7823, paratype, transverse, $\times 2$.	
11, 12. P.R.I. 44703, 11. transverse, $\times 2$; 12. longitudinal, $\times 2$.	
13. P.R.I. 44704, longitudinal, $\times 2$.	
14, 15, 16. P.R.I. 44705, 14. transverse, $\times 2$; 15. longitudinal, $\times 2$; 16. longitudinal enlarged with presepiments forming platform, $\times 5$.	



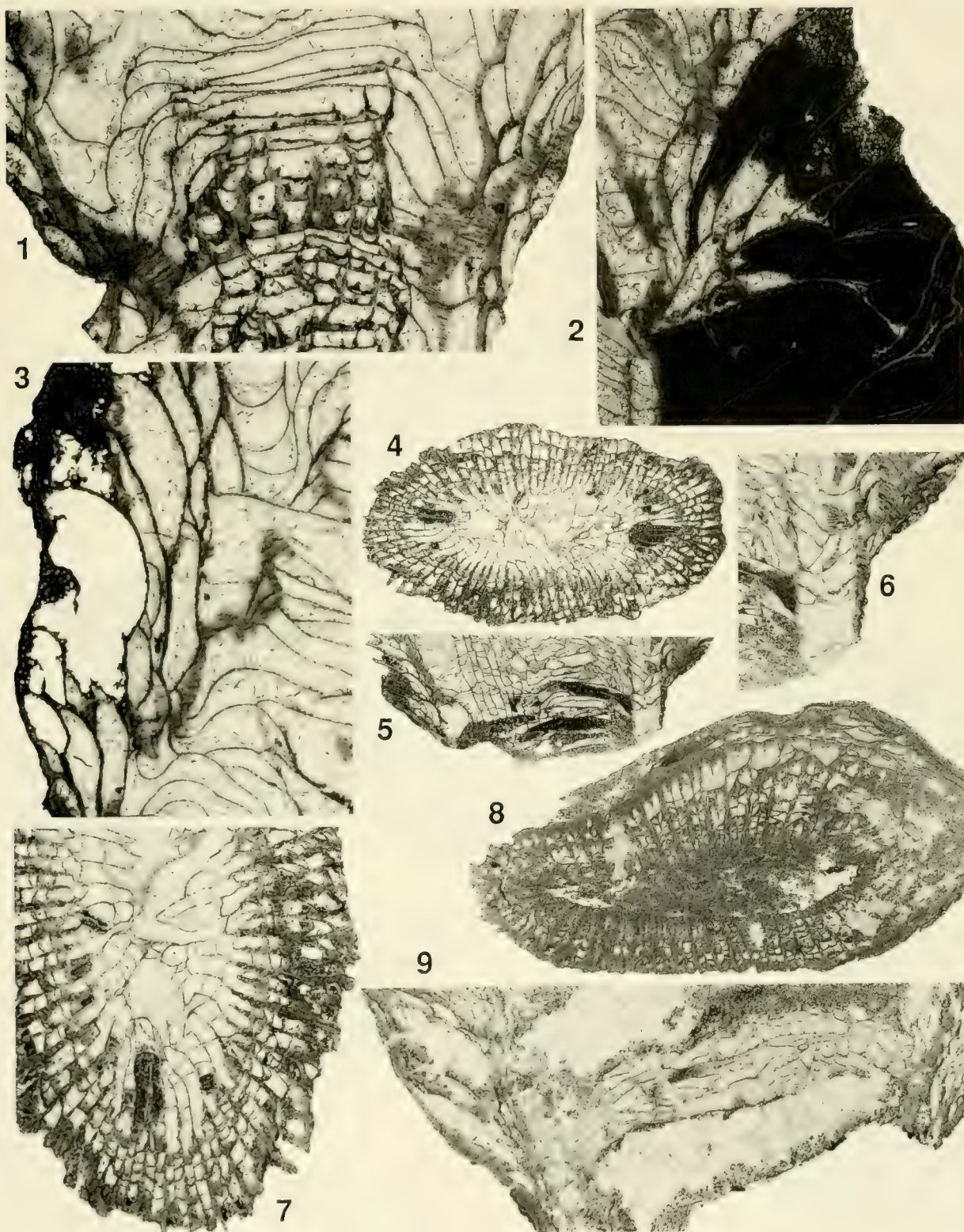


EXPLANATION OF PLATE 8

Figure	Page
1-16. <i>Tabulophyllum rotundum</i> Fenton and Fenton, 1924	36
1, 2. U.M.M.P. 7838, holotype, 1. longitudinal, $\times 2$; 2. transverse, $\times 2$.	
3, 4. F.M.N.H. 26004, paratype, 3. transverse, $\times 2$; 4. longitudinal with flaring of upper part of corallite by expanding dissepimentarium, $\times 2$.	
5, 6. F.M.N.H. 26005, paratype, 5. transverse, $\times 2$; 6. longitudinal with large presepiments, $\times 2$.	
7. P.R.I. 44706, longitudinal of specimen with extravagant development of presepiments, $\times 3$.	
8, 9. P.R.I. 44707, 8. transverse, $\times 2$; 9. longitudinal with preferential development of presepiments on convex side of corallite, $\times 2$.	
10. P.R.I. 44708, transverse, $\times 4$.	
11, 12. P.R.I. 44709, 11. longitudinal, $\times 2$; 12. transverse, $\times 2$.	
13. P.R.I. 44710, longitudinal, $\times 2$.	
14, 15. P.R.I. 44711, 14. transverse, $\times 2$; 15. longitudinal, $\times 2$.	
16. P.R.I. 44712, longitudinal, with preferential development of presepiments on convex side of corallite, $\times 2$.	

EXPLANATION OF PLATE 9

Figure	Page
1-3. <i>Tabulophyllum rotundum</i> Fenton and Fenton, 1924	36
1. P.R.I. 44713, enlarged longitudinal view to illustrate amplexoid septa and trabecular structure, $\times 10$.	
2. P.R.I. 44711, longitudinal, enlarged from Plate 5, figure 6, to show thin, delicate nature of presepiments in shale matrix, $\times 7.5$.	
3. P.R.I. 44714, longitudinal, enlarged to illustrate configuration of trough surrounding tabularium, as seen in cross section, $\times 7.5$.	
4-9. <i>Tabulophyllum ellipticum</i> (Hall and Whitfield, 1873)	37
4-7. U.S.N.M. 78624, Fentons' neotype, 4. transverse, $\times 2$; 5. longitudinal, $\times 2$; 6. longitudinal enlarged to illustrate fine septal trabeculae, $\times 4$; 7. transverse, enlarged to show cardinal area, $\times 4$.	
8, 9. P.R.I. 44715, 8. transverse, $\times 2$; 9. longitudinal with recrystallized areas, $\times 2.5$.	



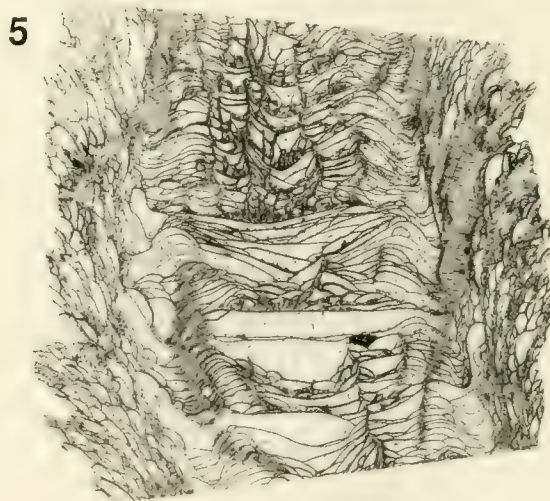
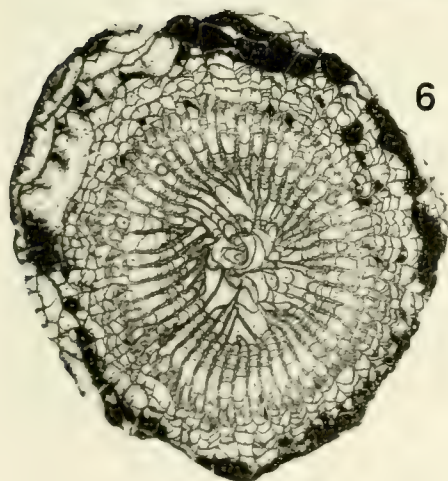
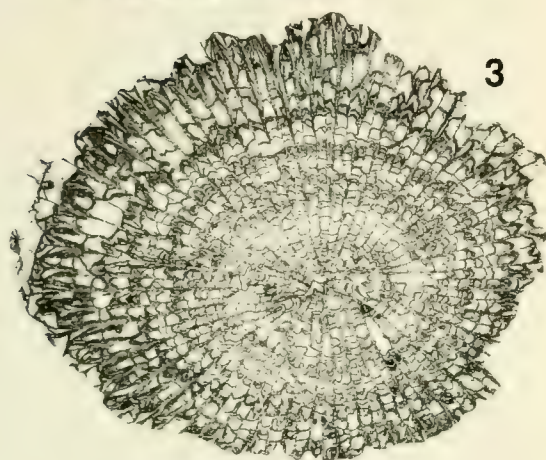
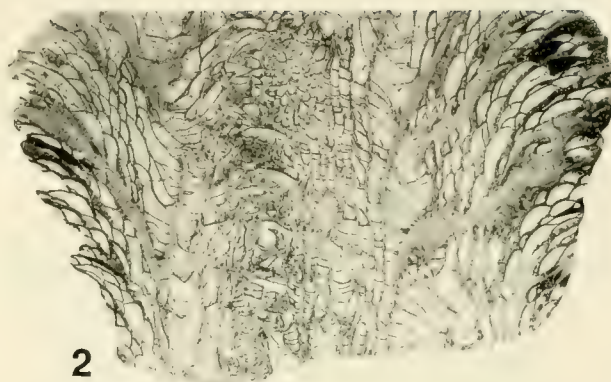
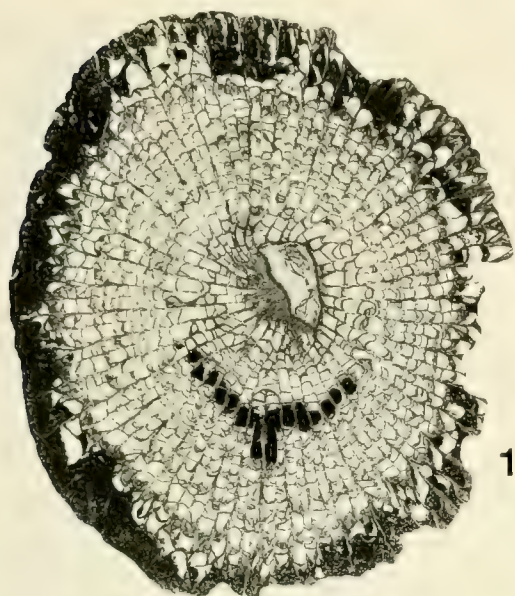


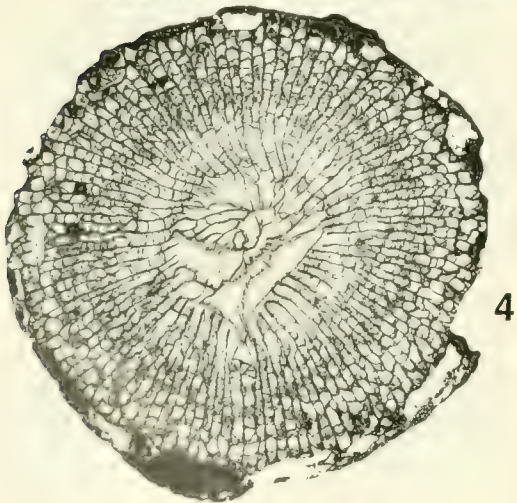
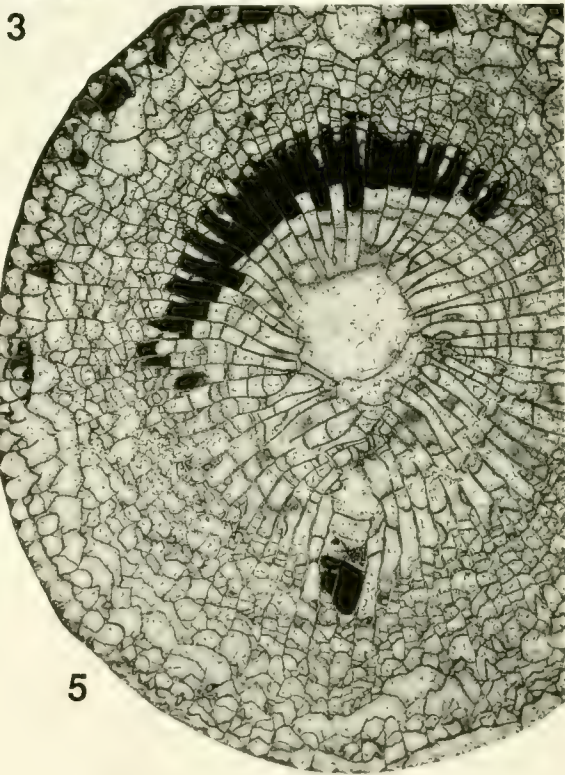
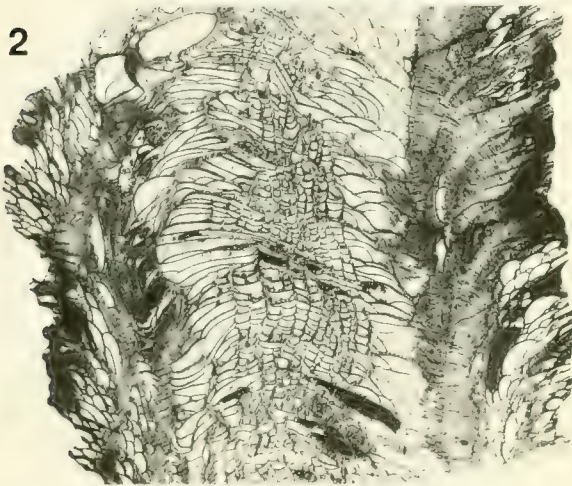
EXPLANATION OF PLATE 10

Figure	Page
1-2. <i>Tabulophyllum ponderosum</i> Fenton and Fenton, 1924	38
1, 2. U.S.N.M. 78623a, holotype, 1. transverse with cardinal area at bottom of photograph, $\times 1.5$; 2. longitudinal, $\times 1.5$	
3-8. <i>Tabulophyllum robustum</i> Fenton and Fenton 1924	39
All transverse sections oriented with cardinal area at bottom.	
3, 4. U.S.N.M. 78632A, holotype, 3. transverse, $\times 2$; 4. longitudinal of broad tabularium and preferential development of dissepimentarium at left, $\times 2$. 5, 6. U.S.N.M. 78632, paratype, 5. transverse, $\times 2$; 6. longitudinal with flat-topped tabulae, $\times 2$.	
7, 8. U.S.N.M. 78444a, 7. transverse, $\times 2$; 8. transverse of younger part of corallite, $\times 2$.	
9, 10. F.M.N.H. 26007, holotype, <i>Tabulophyllum exiguum</i> Fenton and Fenton 1924, here synonymized. 9. transverse with cardinal area at bottom, $\times 2$; 10. longitudinal, with presepiments best developed on convex side, $\times 2$.	

EXPLANATION OF PLATE 11

Figure	Page
1-6. <i>Tabulophyllum longum</i> Fenton and Fenton, 1924	39
1, 2. F.M.N.H. 26011, holotype, 1. transverse, $\times 2$; 2. longitudinal with marked peripheral gutter in tabularium, $\times 2$.	
3. U.S.N.M. 78634A, transverse of paratype, $\times 2$.	
4, 5. S.U.I. 3629B, 4. transverse of corallite with weak bilaterality, $\times 2$; 5. longitudinal with tabularial gutters and fragmentary tabular segments draped over amplexoid septa, $\times 2$.	
6. U.S.N.M. 78634, transverse of juvenile stage in paratype, $\times 2$.	



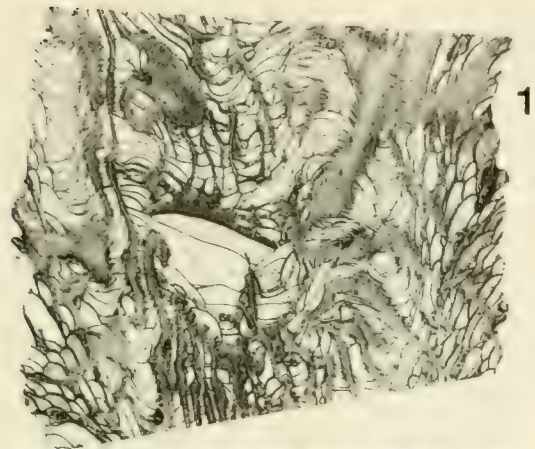


EXPLANATION OF PLATE 12

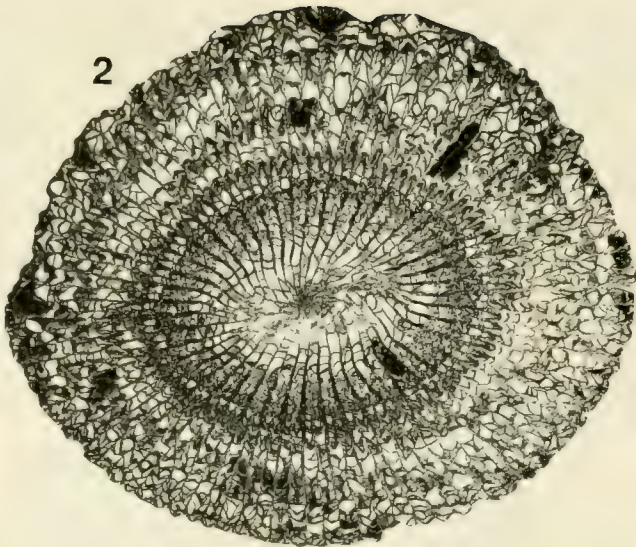
Figure	Page
1-5. <i>Tabulophyllum longum</i> Fenton and Fenton, 1924	39
1. U.S.N.M. 78634, longitudinal of paratype, $\times 2$.	
2, 3. U.S.N.M. 53183, 2. longitudinal, $\times 2$; 3. enlarged to illustrate septal trabeculae, $\times 5$.	
4. P.R.I. 44716, transverse of corallite with short cardinal septum, at bottom, $\times 2$.	
5. P.R.I. 44717, transverse of specimen with slight bilaterality of septa, $\times 2.5$.	

EXPLANATION OF PLATE 13

Figure	Page
1. <i>Tabulophyllum longum</i> Fenton and Fenton, 1924	39
1. S.U.I. 3076-3, longitudinal, with amplexoid septa on prominent tabula above large open space in center of photograph, and with tabularial gutter at left side of photo, $\times 2$.	
2-7. <i>Tabulophyllum magnum</i> Fenton and Fenton, 1924	41
2, 3, 4. F.M.N.H. 26009, holotype, 2. transverse, $\times 1.5$; 3. longitudinal, $\times 1.5$; 4. enlarged longitudinal showing broad dissepimentarium, $\times 2.5$.	
5, 6. U.S.N.M. 78638, paratype, 5. transverse, $\times 2$; 6. longitudinal, $\times 2$.	
7. S.U.I. 3632-2, juvenile with differentiated cardinal septum at bottom, transverse, in this case photographed from the underside, accounting for apparent difference from normal septal deflection, $\times 2$.	



1



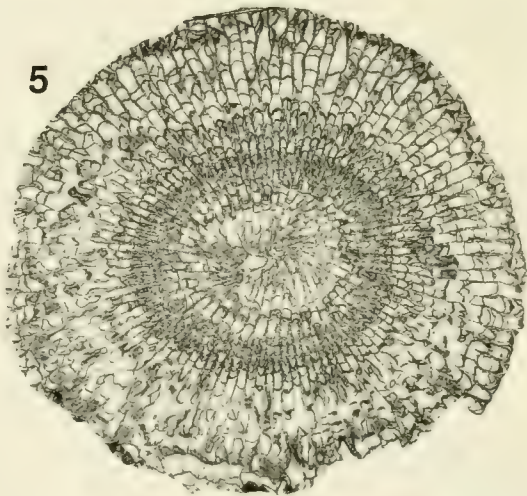
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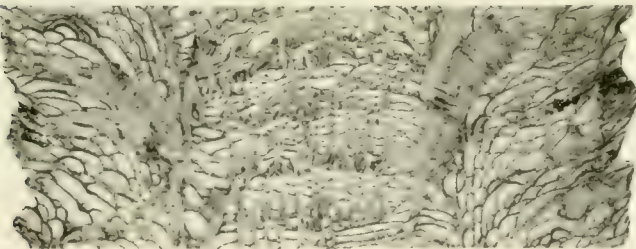
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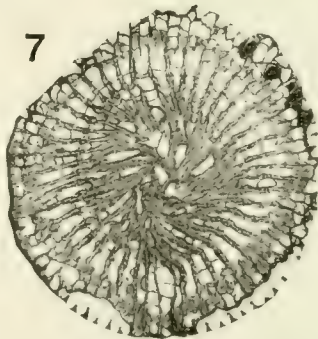
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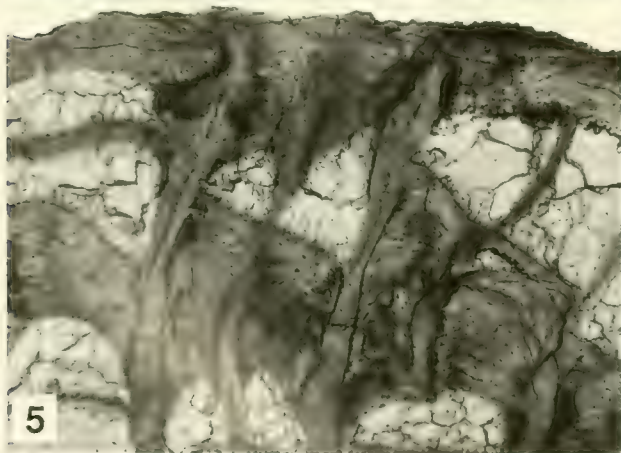
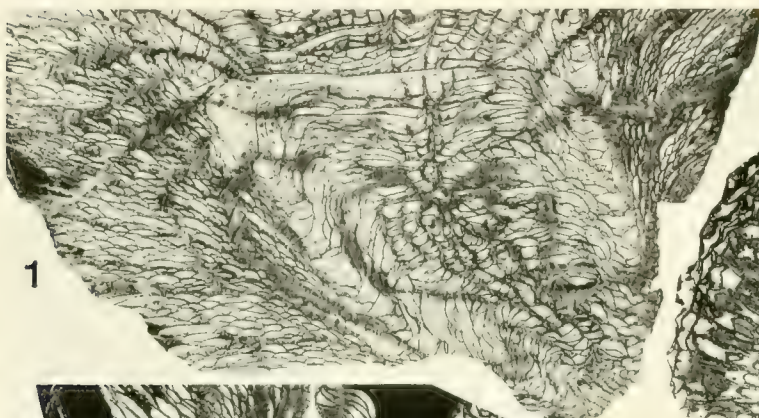
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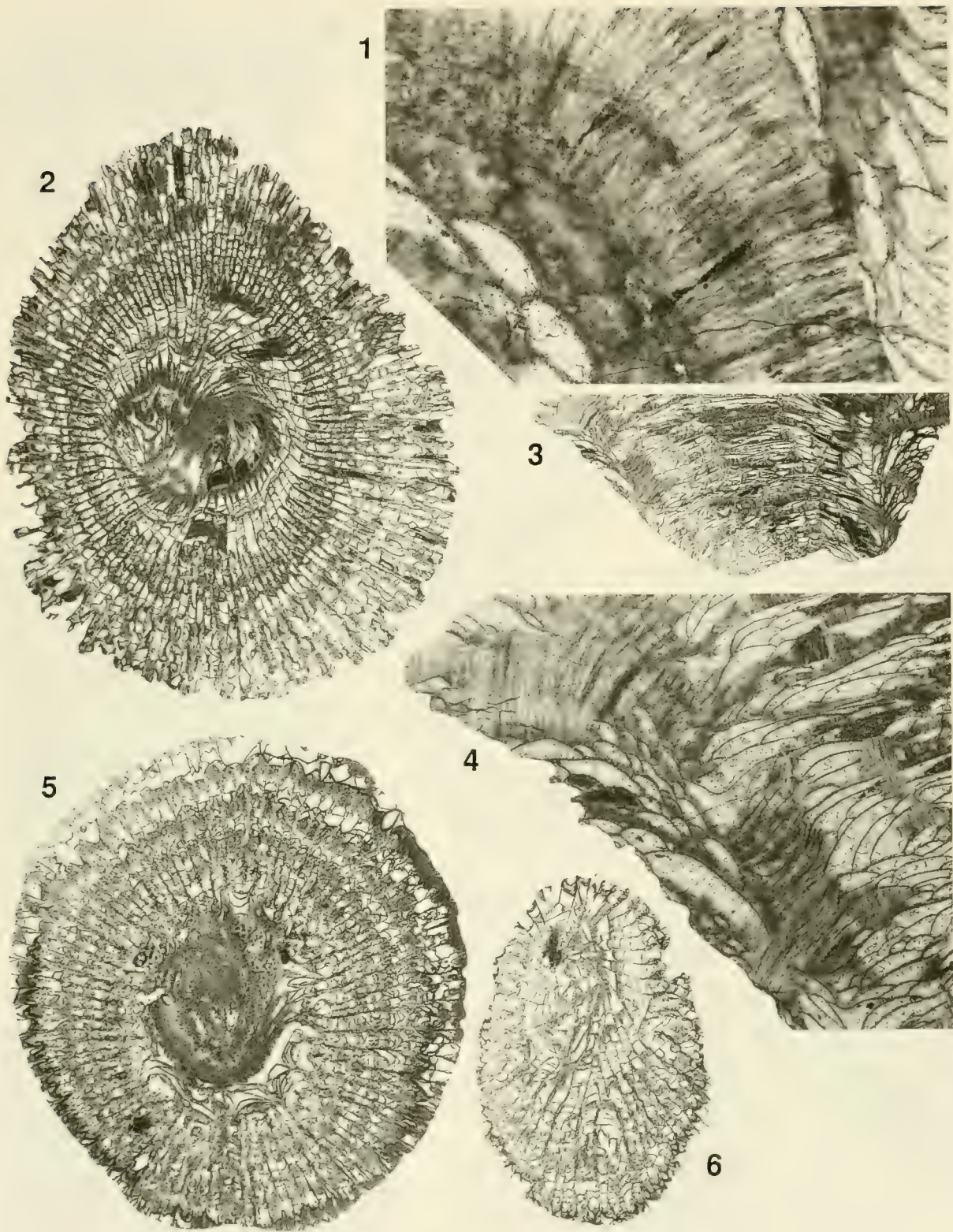


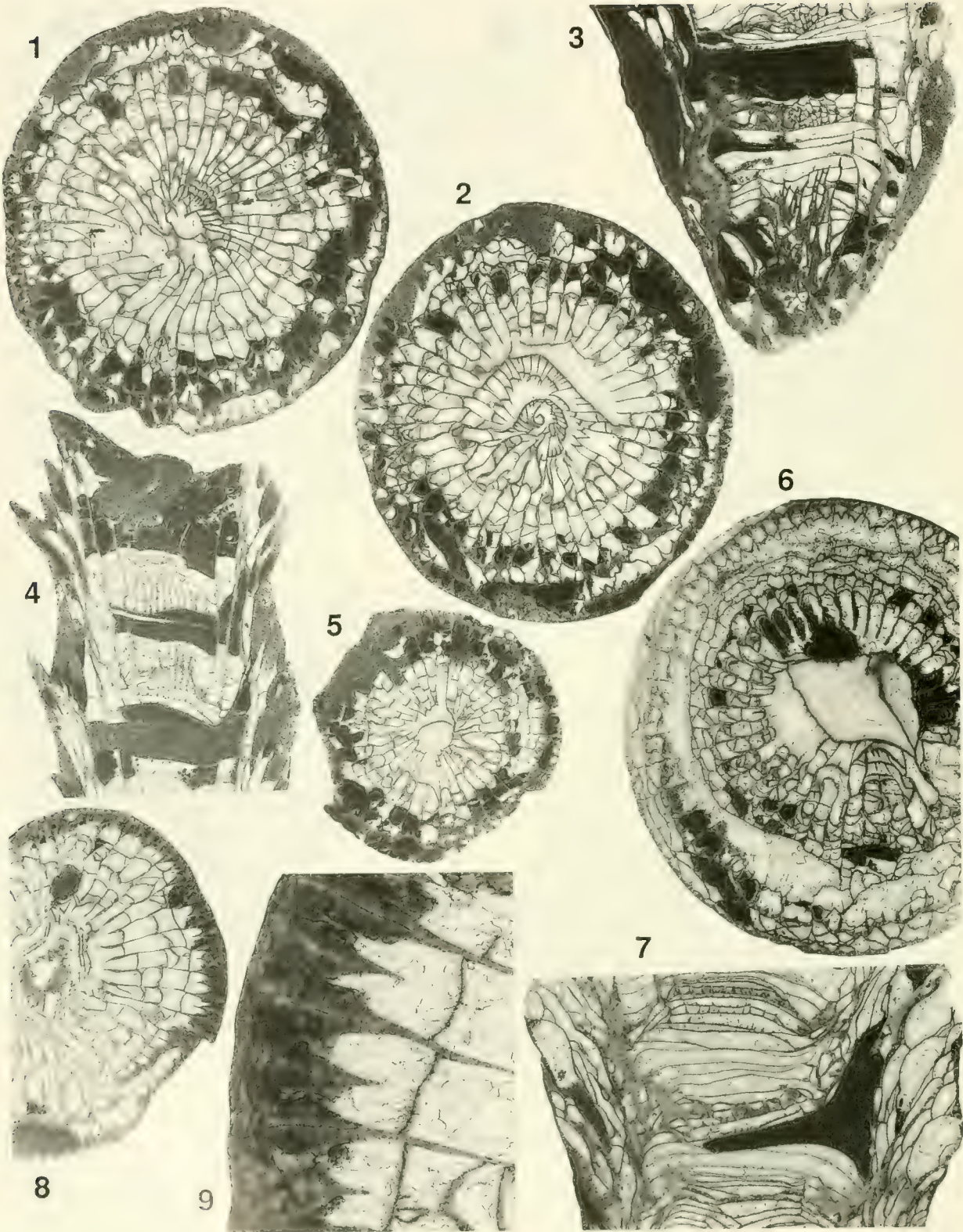
EXPLANATION OF PLATE 14

Figure	Page
1-5. <i>Tabulophyllum magnum</i> Fenton and Fenton, 1924	41
1. S.U.I. 3621, longitudinal of large individual with broadly expanding dissepimentarium, $\times 1.5$.	
2, 3. P.R.I. 44718, a very large specimen with remarkable expansion and contraction of dissepimentarium resulting from variable sedimentation, 2. transverse, $\times 1.5$; 3. longitudinal with amplexoid septa and heavy tabulae related to expansions and contractions of lonsdaleoid dissepimentarium, $\times 1.5$.	
4. S.U.I. 3621, transverse, illustrating growth increments within monacanthine septa, $\times 25$.	
5. P.R.I. 44719, transverse, illustrating (diagenetic) lamellar skeletal structures, $\times 25$.	

EXPLANATION OF PLATE 15

Figure	Page
1. <i>Tabulophyllum magnum</i> Fenton and Fenton, 1924	41
1. S.U.I. 3623, longitudinal, enlarged to show septal trabecular structure, $\times 10$.	
2-6. <i>Tabulophyllum expansum</i> Fenton and Fenton, 1924	43
2, 3, 4. F.M.N.H. 26012, holotype of species, 2. transverse with cardinal area at bottom and prominent axial boss, $\times 1.5$; 3. longitudinal, $\times 1.5$; 4. longitudinal enlarged to illustrate septal structure, $\times 5$.	
5, 6. S.U.I. 3339, specimen collected by Belanski, transverse sections oriented so that cardinal is at bottom, 5. transverse, $\times 2$; 6. transverse in juvenile part of corallite with clearly differentiated cardinal area, $\times 2$.	



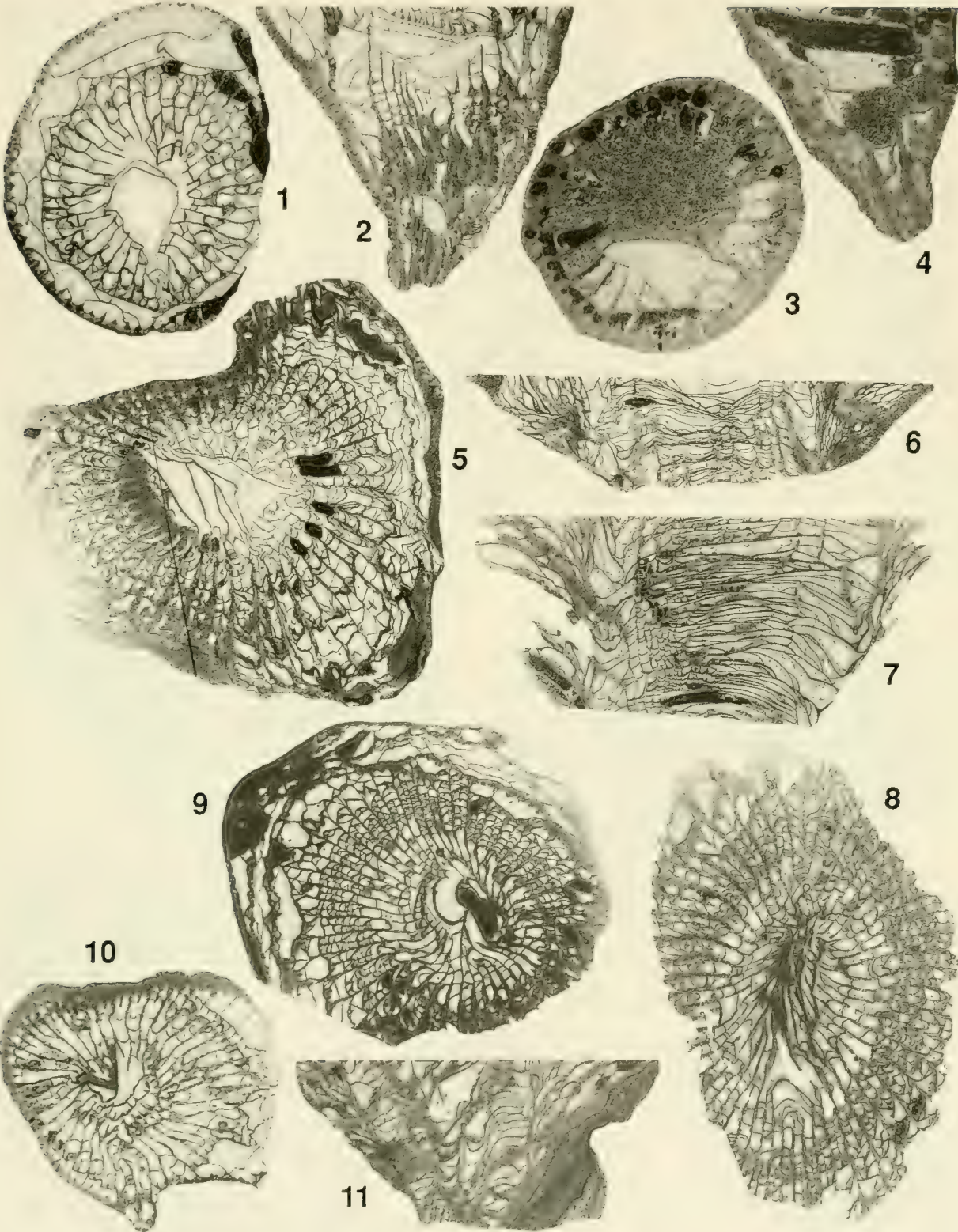


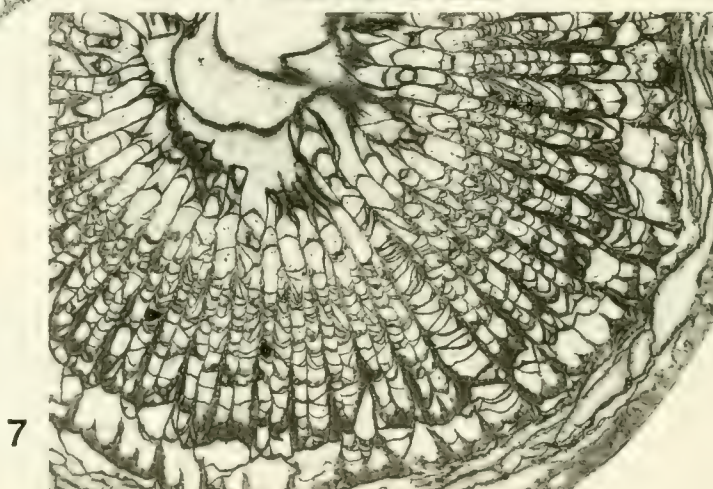
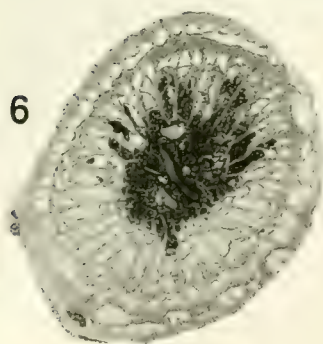
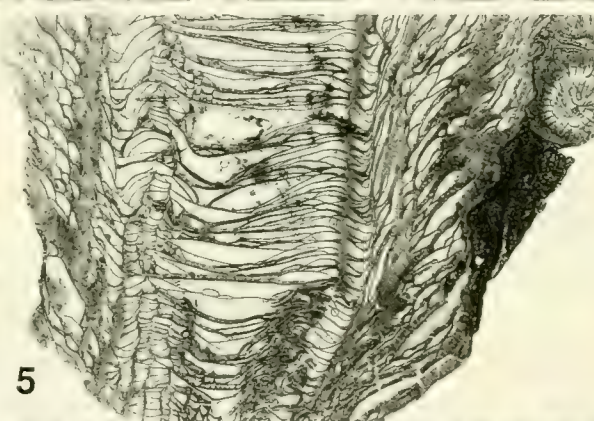
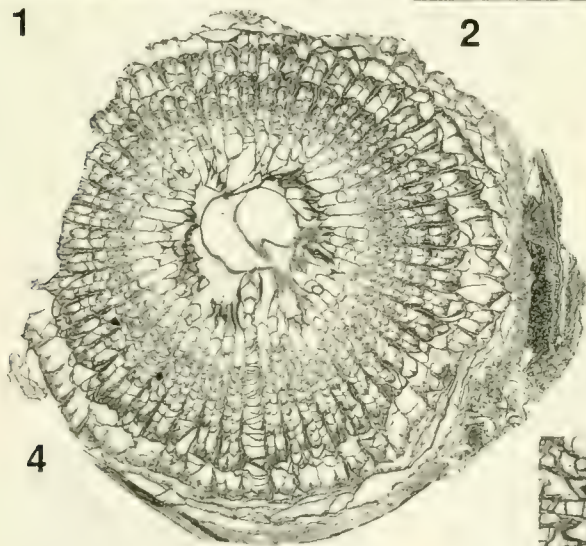
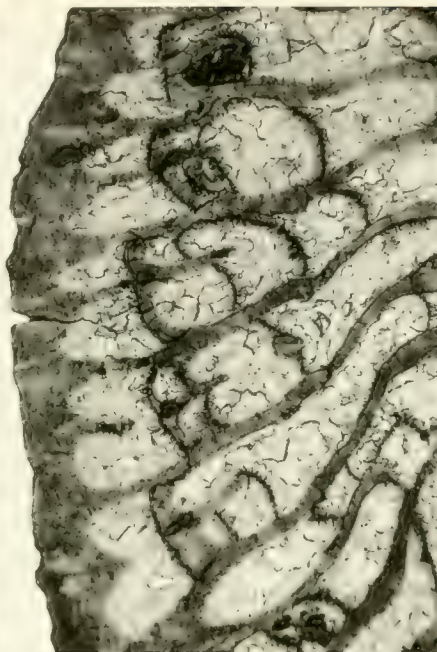
EXPLANATION OF PLATE 16

Figure	Page
1-9. <i>Tabulophyllum mutabile</i> n. sp.	44
1, 2, 3. S.U.I. 2247, holotype, 1. transverse, high in corallite, just beneath calice, $\times 2$; 2. transverse lower in corallite, showing amplexoid septa abutting tabulae, $\times 2$; longitudinal with sediment infilling some presepiments and amplexoid septa based on tabulae, $\times 2$.	
4, 5. S.U.I. 1731, paratype, 4. longitudinal of corallite with sediment infilling skeletal space and resulting expansion of dissepimentarium, $\times 2$; 5. transverse showing short cardinal septum, $\times 2$.	
6, 7. S.U.I. 141, paratype, 6. transverse of large individual with large presepiments, $\times 2$; longitudinal showing large, bulbous presepiments at right, $\times 2$.	
8, 9. S.U.I. 84745, paratype, 8. transverse of corallite (photographed from underside) with heavy outer wall, $\times 2$; 9. enlarged view of wall with septothecal structure, $\times 9$.	

EXPLANATION OF PLATE 17

Figure	Page
1-4. <i>Tabulophyllum mutabile</i> n. sp.	44
1, 2. S.U.I. 431, paratype, 1. transverse, corallite with apparent cardinal area, $\times 2$; 2. longitudinal with large intertabular spaces, $\times 2$.	
3, 4. P.R.I. 44720, 3. transverse of corallite with large amount of sediment infilling skeletal openings, $\times 2$; 4. longitudinal, $\times 2$.	
5-11. <i>Tabulophyllum curtum</i> n. sp.	45
5, 6. P.R.I. 44721, holotype, 5. transverse, showing compressed and indented left and upper side, $\times 1.25$; 6. longitudinal with characteristic broad, arched tabularium, $\times 1.25$.	
7, 8. S.U.I. 707, paratype, an undeformed corallite, 7. longitudinal, $\times 2$; 8. transverse, $\times 2$.	
9. S.U.I. 1435, paratype, transverse of corallite expanding towards left, $\times 2$.	
10, 11. S.U.I. 853, paratype, 10. transverse of corallite growing on square object in lower right corner, $\times 1.5$; 11. longitudinal with preferential growth toward left, $\times 1.5$.	



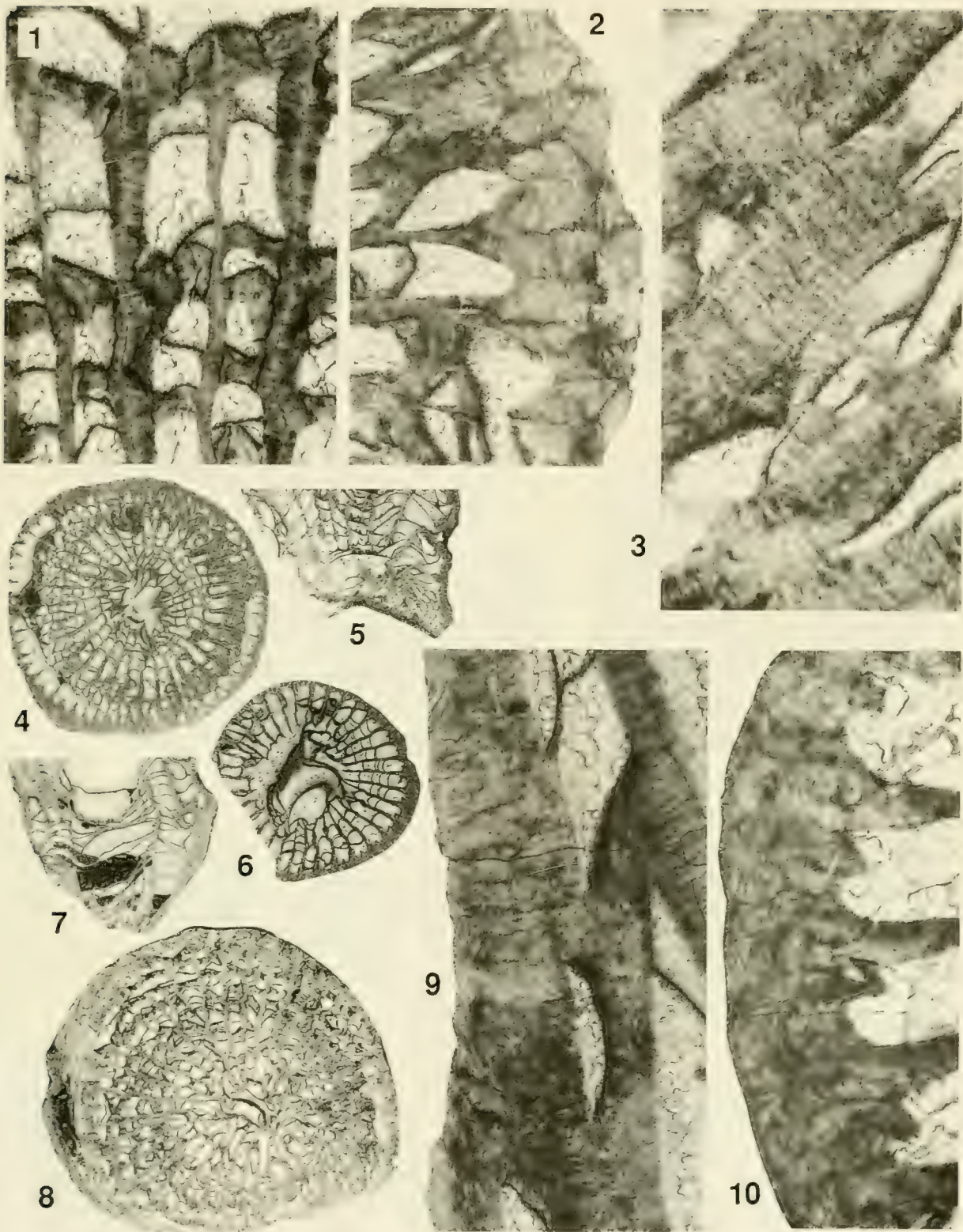


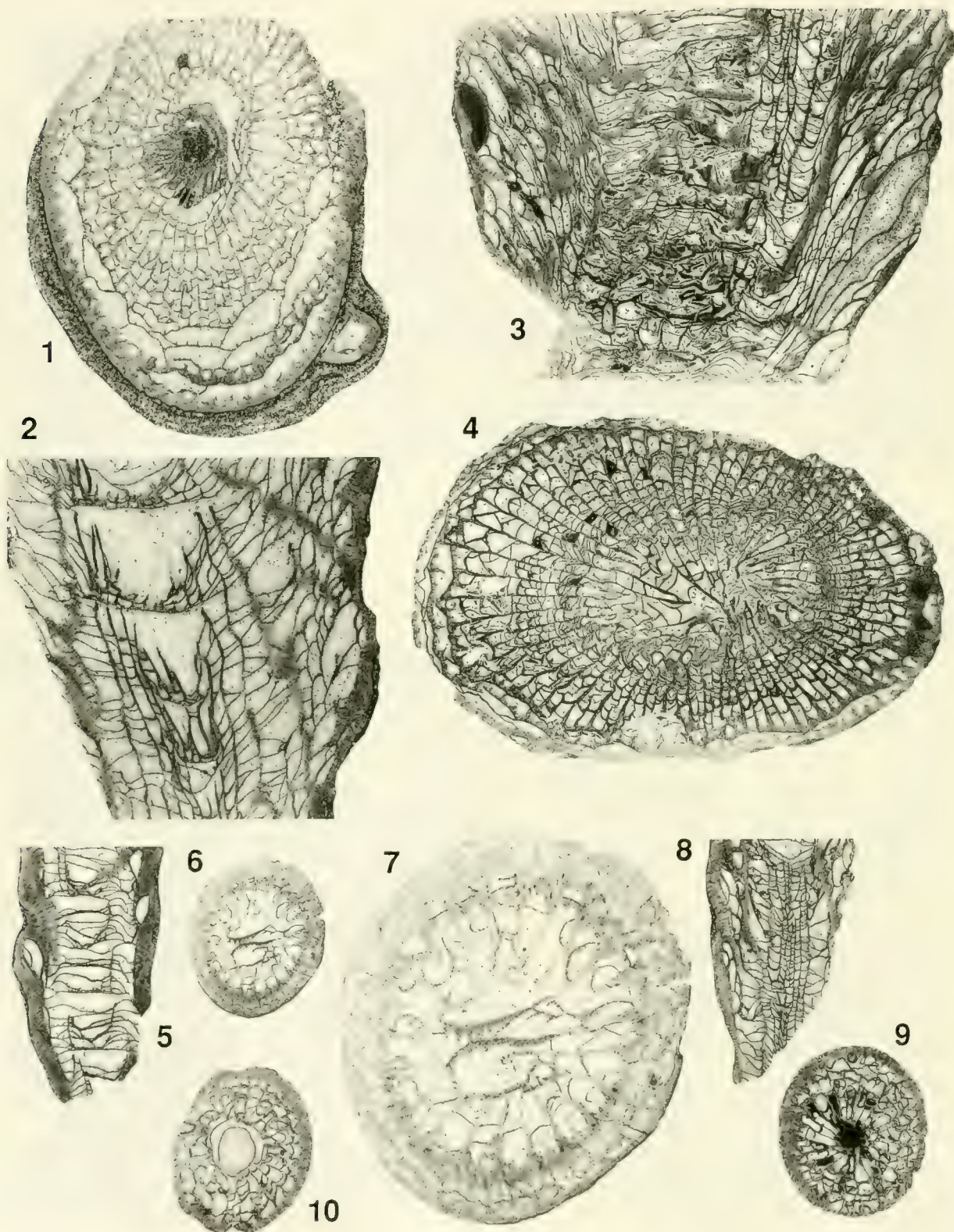
EXPLANATION OF PLATE 18

Figure	Page
1-3. <i>Tabulophyllum curtum</i> n. sp.	45
1. P.R.I. 44722, paratype, transverse of septal structure with very fine trabeculae and fibro-normal flanks, $\times 12$.	
2. S.U.I. 1435, transverse of septotheca, $\times 10$.	
3. P.R.I. 44721, holotype, transverse, to illustrate growth lines in tangential section of dissepiment, $\times 10$.	
4-7. <i>Tabulophyllum levorsoni</i> n. sp.	46
4-7. P.R.I. 44723, holotype, 4. transverse, $\times 1.5$; 5. longitudinal, $\times 1.5$; 6. transverse of juvenile portion of holotype, $\times 2$; 7. transverse section, enlarged to show cardinal area with "ladder-like" intersections with dissepiments, $\times 2.5$.	

EXPLANATION OF PLATE 19

Figure	Page
1-3. <i>Tabulophyllum levorsoni</i> n. sp.	46
1-3. P.R.I. 44723, holotype, 1. transverse of fibro-normal, fine trabecular septal structure, $\times 12$; 2. transverse of septotheca with some diagenetic modification in outer part of wall, $\times 12$; 3. longitudinal of septal microstructure with fine trabecular and incremental growth, $\times 12$.	
4-10. <i>Tabulophyllum buccinum</i> n. sp.	47
4, 5. S.U.I. 1282, holotype, 4. transverse, with few, very elongate presepiments, $\times 2$; 5. longitudinal, $\times 2$.	
6, 7. S.U.I. 1255, paratype with little or no lonsdaleoid dissepimentarium, 6. transverse, $\times 2$; 7. longitudinal, $\times 2$.	
8. P.R.I. 44728, paratype with uncharacteristic large number of long septa, transverse, $\times 2$.	
9. S.U.I. 1033, longitudinal of lath-like increments to septotheca and septal trabeculae at right, $\times 15$.	
10. S.U.I. 1285, paratype, transverse of septotheca, $\times 15$.	



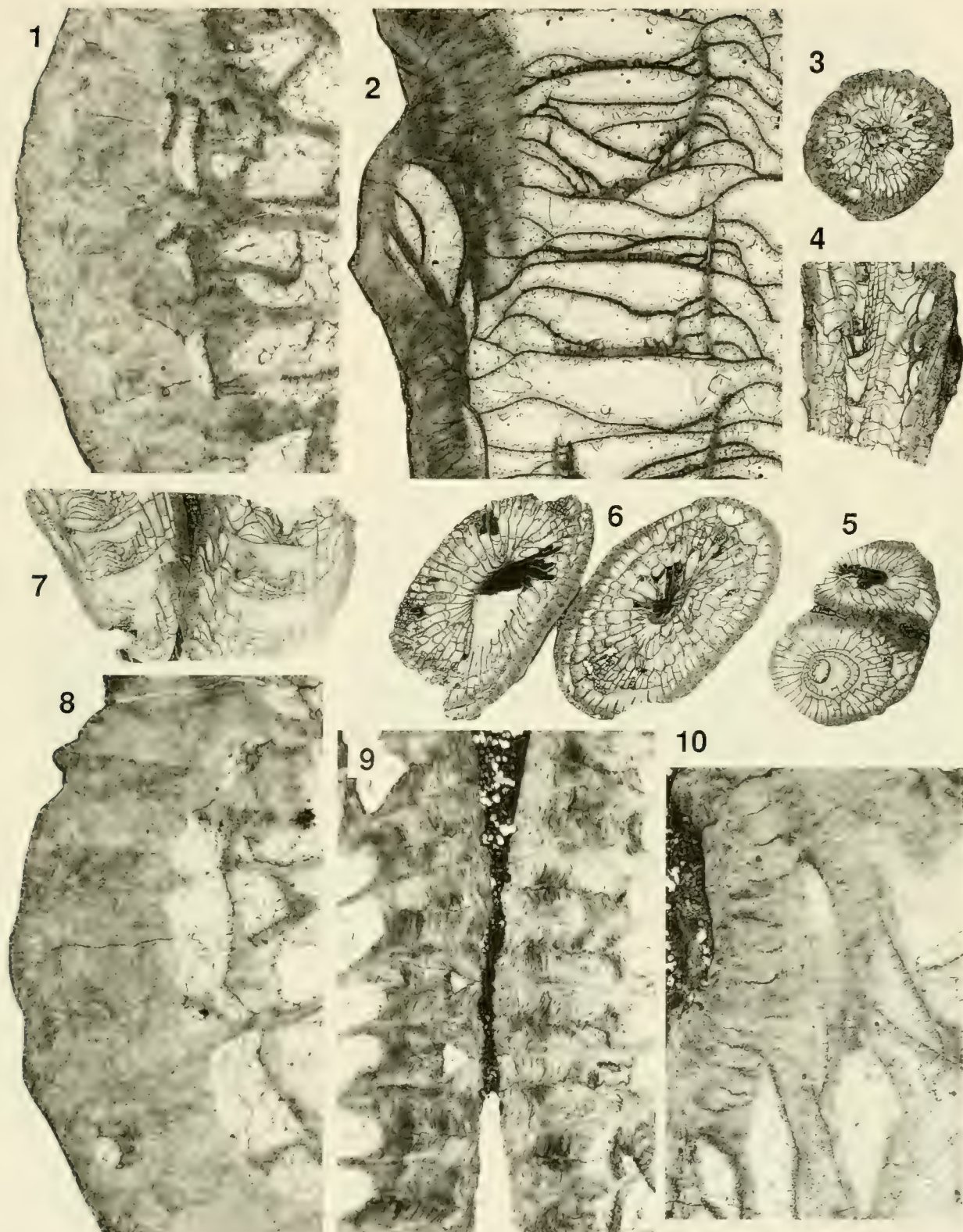


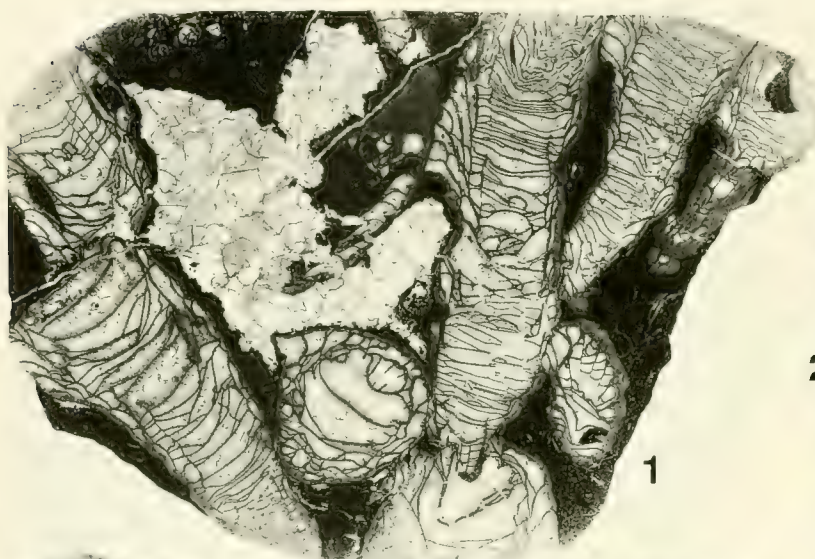
EXPLANATION OF PLATE 20

Figure	Page
1-2. <i>Tabulophyllum</i> sp. A	48
1, 2. P.R.I. 44729, 1. transverse of ovoid corallite with elongate presepiments, $\times 3$; 2. longitudinal with amplexoid septa based on sparse tabulae, $\times 3$.	
3-4. <i>Tabulophyllum</i> sp. B	48
3, 4. S.U.I. 186, 3. longitudinal, with large presepiments, $\times 2$; 4. transverse of corallite with arrow-like septa, thickest at presepimental wall, $\times 2$.	
5-10. <i>Tarphyphyllum cylindricum</i> n. sp.	49
5, 6, 7. S.U.I. 1291, holotype, 5. longitudinal, with complete, arcuate tabulae and few dissepiments, $\times 2$; 6. transverse with short septa, $\times 2$; 7. transverse, enlarged to show septotheca, $\times 5$.	
8, 9. S.U.I. 1250, paratype, 8. longitudinal, $\times 2$; 9. transverse of corallite with long septa, $\times 2$.	
10. P.R.I. 44730, paratype, transverse, $\times 2$.	

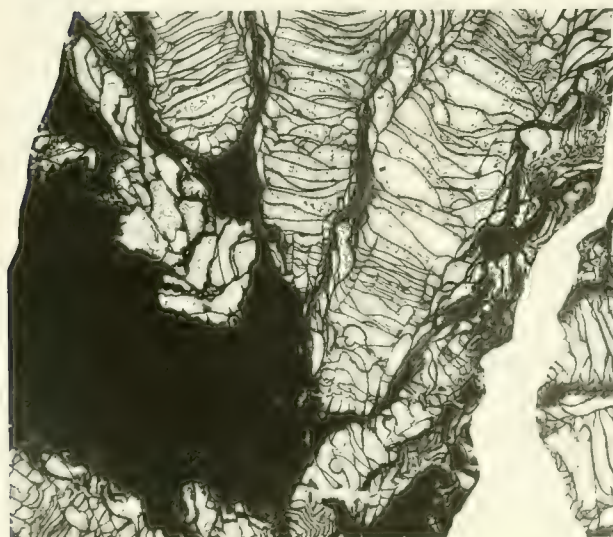
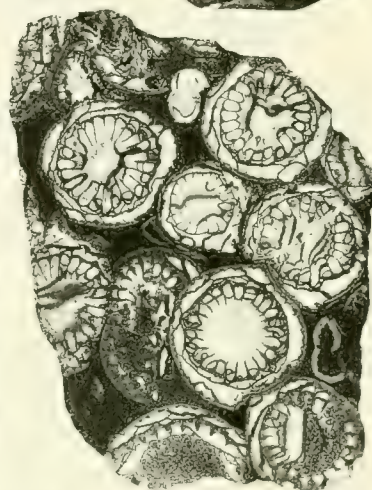
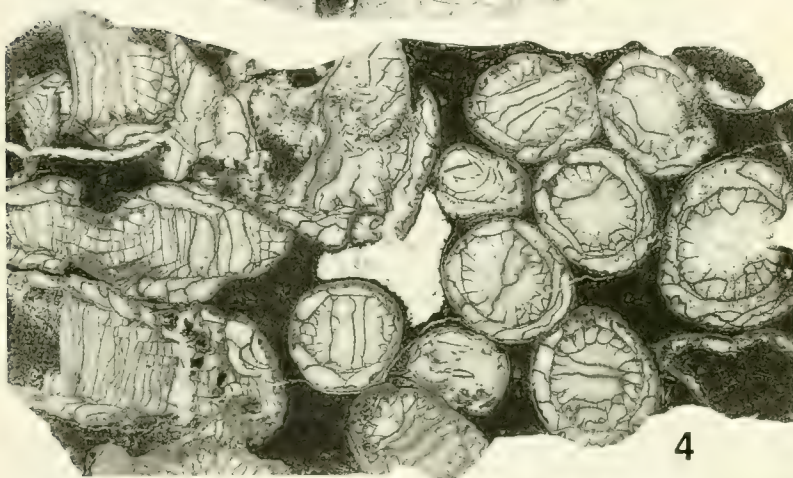
EXPLANATION OF PLATE 21

Figure	Page
1-4, 8. <i>Tarphyphyllum cylindricum</i> n. sp.	49
1, 2. S.U.I. 1291, holotype, 1. transverse, enlarged of septothecal wall structure, $\times 14$; 2. longitudinal, enlarged wall and septal structure, $\times 7$.	
3, 4. S.U.I. 1290, paratype, 3. transverse, $\times 2$; 4. longitudinal, $\times 2$.	
8. P.R.I. 44731, paratype, transverse, enlarged of wall and septal structure, $\times 16$.	
5-7, 9, 10. <i>Tarphyphyllum</i> sp. A	50
5, 6, 7, 9, 10. S.U.I. 84748, 5. twinned juvenile, transverse, $\times 2$; 6. adult transverse, $\times 2$; longitudinal of corallites with sparse tabulae, $\times 2$; 9. transverse, enlarged to show slightly (diagenetically) modified wall and septal structure, $\times 12$; 10. longitudinal, enlarged to show wall structure and septal trabeculae, $\times 12$.	



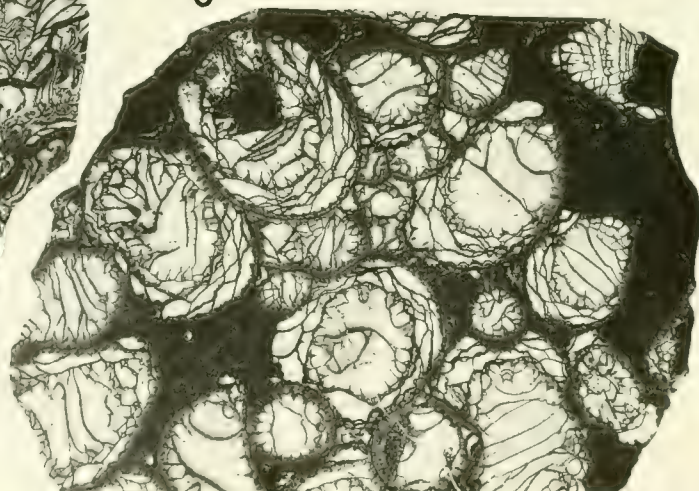


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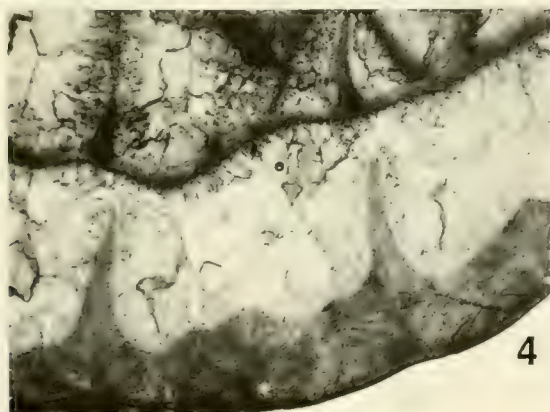
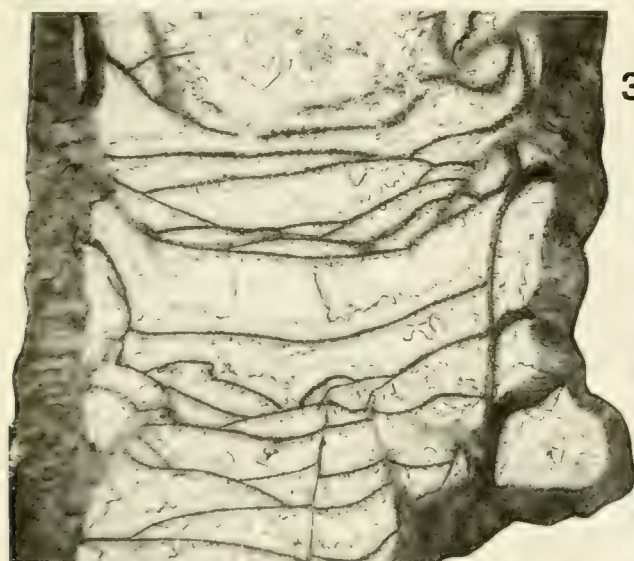
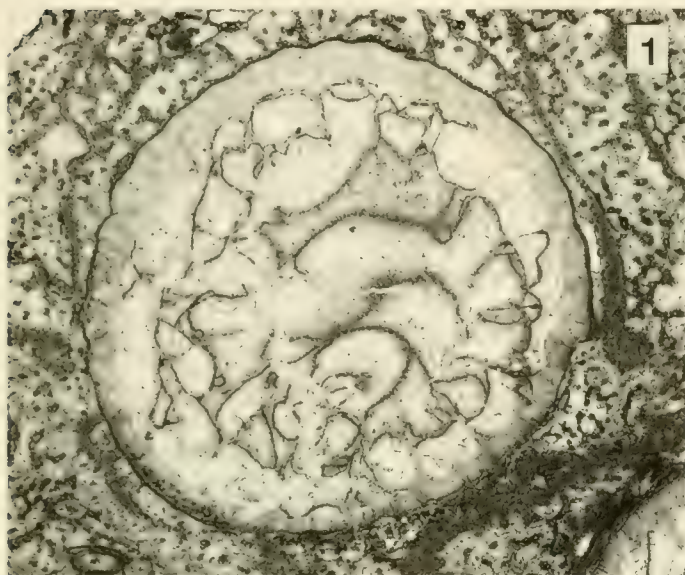


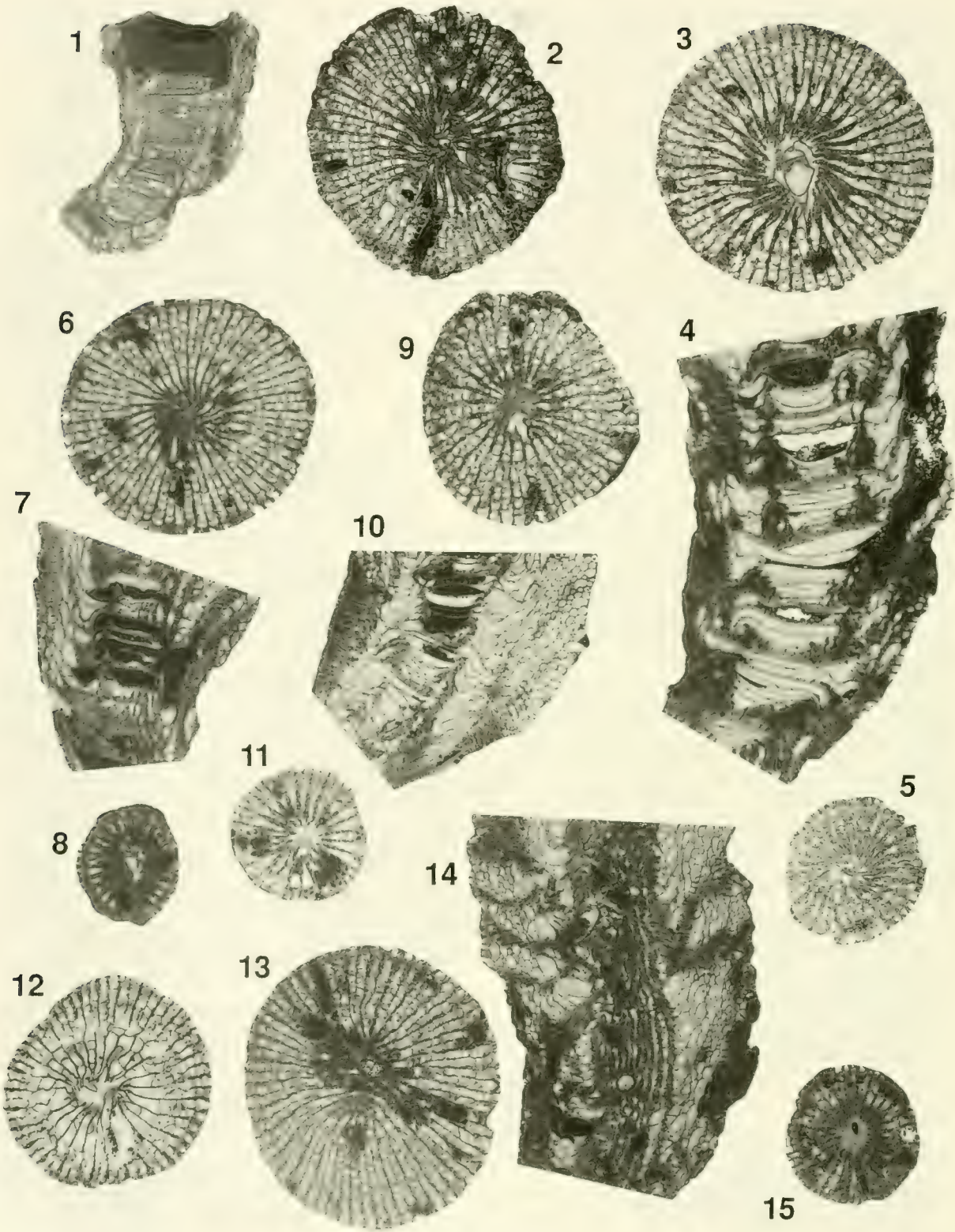
EXPLANATION OF PLATE 22

Figure	Page
1-6. <i>Smithiphyllum belanskii</i> Pedder, 1965	51
1, 2. S.U.I. 11616, holotype, 1. longitudinal, illustrating tabulae that are complete, flat or sagging, or incomplete and inclined, × 2; 2. transverse with short, thin septa and elongate presepiments, × 2.	
3. S.U.I. 11617, paratype, transverse, with prominent presepiments, × 2.	
4. S.U.I. 84749, transverse and longitudinal of topotype, × 2.	
5, 6. P.R.I. 44732, 5. longitudinal, with irregular tabulae, × 2; 6. transverse with numerous buds, × 2.	

EXPLANATION OF PLATE 23

Figure	Page
1-5. <i>Smithiphyllum belanskii</i> Pedder, 1965	51
1. S.U.I. 11617, paratype, transverse, with stromatoporoid ground mass, $\times 8$.	
2. S.U.I. 11616, holotype, enlarged to show dissepiments and septal trabeculae, $\times 15$.	
3. S.U.I. 84749, enlarged to show tabulae and presepiments, $\times 10$.	
4. P.R.I. 44733, enlarged septotheca and short, spine-like septa, $\times 25$.	
5. P.R.I. 44734, longitudinal, with steeply inclined presepiments and variable tabulae, $\times 7$.	



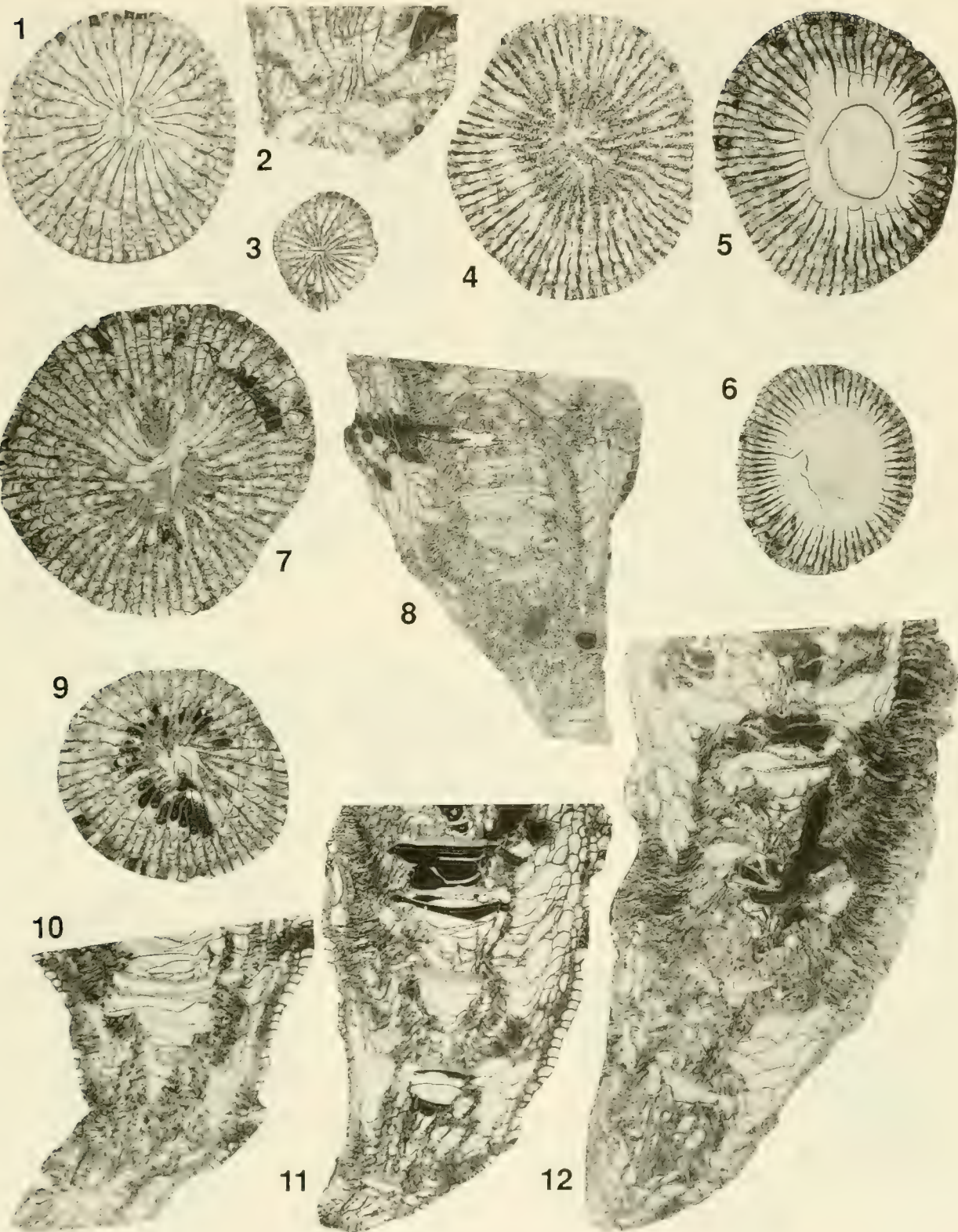


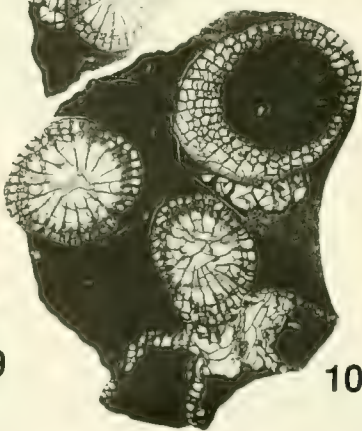
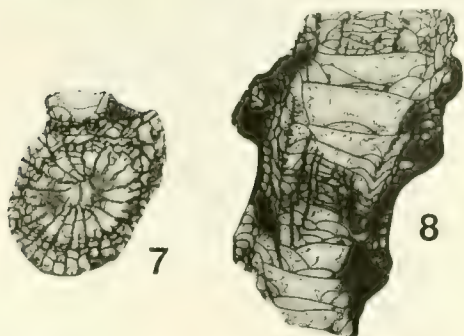
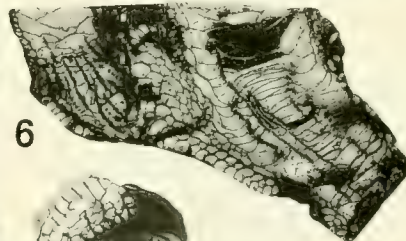
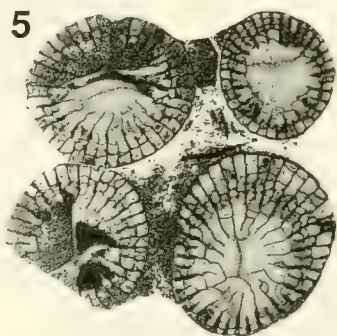
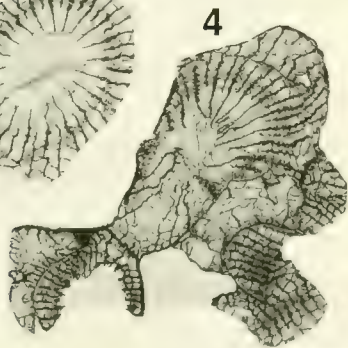
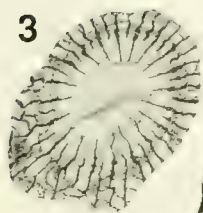
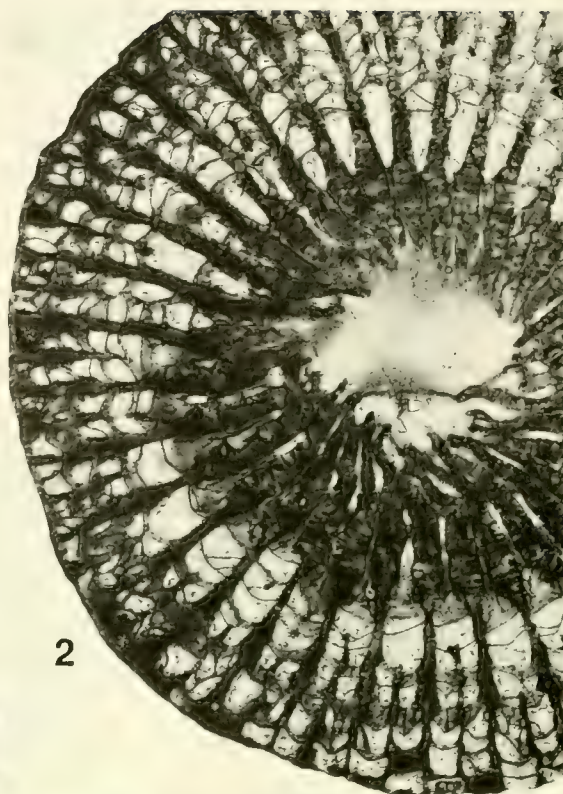
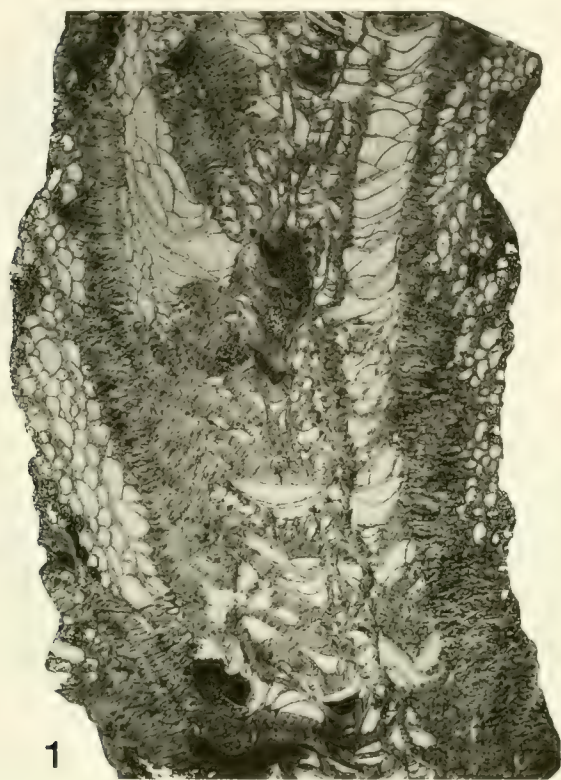
EXPLANATION OF PLATE 24

Figure	Page
1–15. <i>Charactophyllum nanum</i> (Hall and Whitfield, 1873)	54
1. N.Y.S.M. 3160/1, longitudinal acetate peel print of holotype, $\times 2$.	
2. P.R.I. 44739, transverse of individual with long septa dilated in tabularium, $\times 2.5$.	
3–5. P.R.I. 44740, 3. transverse of septal dilation, $\times 2.5$; 4. longitudinal with complete, flat tabulae, $\times 2.5$; 5. juvenile with swirled, dilated septa, $\times 2.5$. Septa in this genus are swirled in a counter-clockwise direction when seen from above. Some photographs on this plate were photographed from below.	
6–8. P.R.I. 44741, 6. transverse, with septa dilated at axis to form boss, $\times 2.5$; 7. longitudinal, $\times 2.5$; 8. juvenile with very heavy septal dilation and short cardinal septum, $\times 2.5$.	
9–11. P.R.I. 44742, 9. transverse, $\times 2.5$; 10. longitudinal with clearly flat-topped tabulae, $\times 2.5$; 11. juvenile, with cardinal septum at bottom of photo, $\times 2.5$.	
12. P.R.I. 44743, transverse of corallite with thin septa, $\times 2.5$.	
13–15. P.R.I. 44744, 13. transverse, $\times 2.5$; 14. longitudinal of corallite with numerous globose dissepiments, $\times 2.5$; 15. juvenile, $\times 2.5$.	

EXPLANATION OF PLATE 25

Figure	Page
1-12. <i>Charactophyllum nanum</i> (Hall and Whitfield, 1873)	54
1, 2, 3. P.R.I. 44745, 1. transverse, $\times 2.5$; 2. longitudinal, $\times 2.5$; 3. juvenile, $\times 2.5$.	
4, 5, 6. P.R.I. 44746, 4. transverse, $\times 2.5$; 5. transverse, $\times 2.5$; 6. transverse, $\times 2.5$; sequence of sections in one corallite illustrating variation in length and dilation of septa.	
7, 8. E.M.N.H. 26002, Fenton "Plesiotype" of <i>Zaphrentis solida</i> , 7. transverse of corallite with knobby septa, $\times 2.5$; 8. longitudinal, $\times 2.5$.	
9. E.M.N.H. 26003, Fenton "Plesiotype", <i>Zaphrentis solida</i> , transverse of corallite with little dilated septa, $\times 2.5$.	
10-13. 10. P.R.I. 44747, longitudinal, $\times 5$; 11. P.R.I. 44748, longitudinal, $\times 5$; and 12. P.R.I. 44749, longitudinal, $\times 4.5$; series to illustrate variation in dissepiments and tabulae and to show pattern of bending in septal trabeculae.	



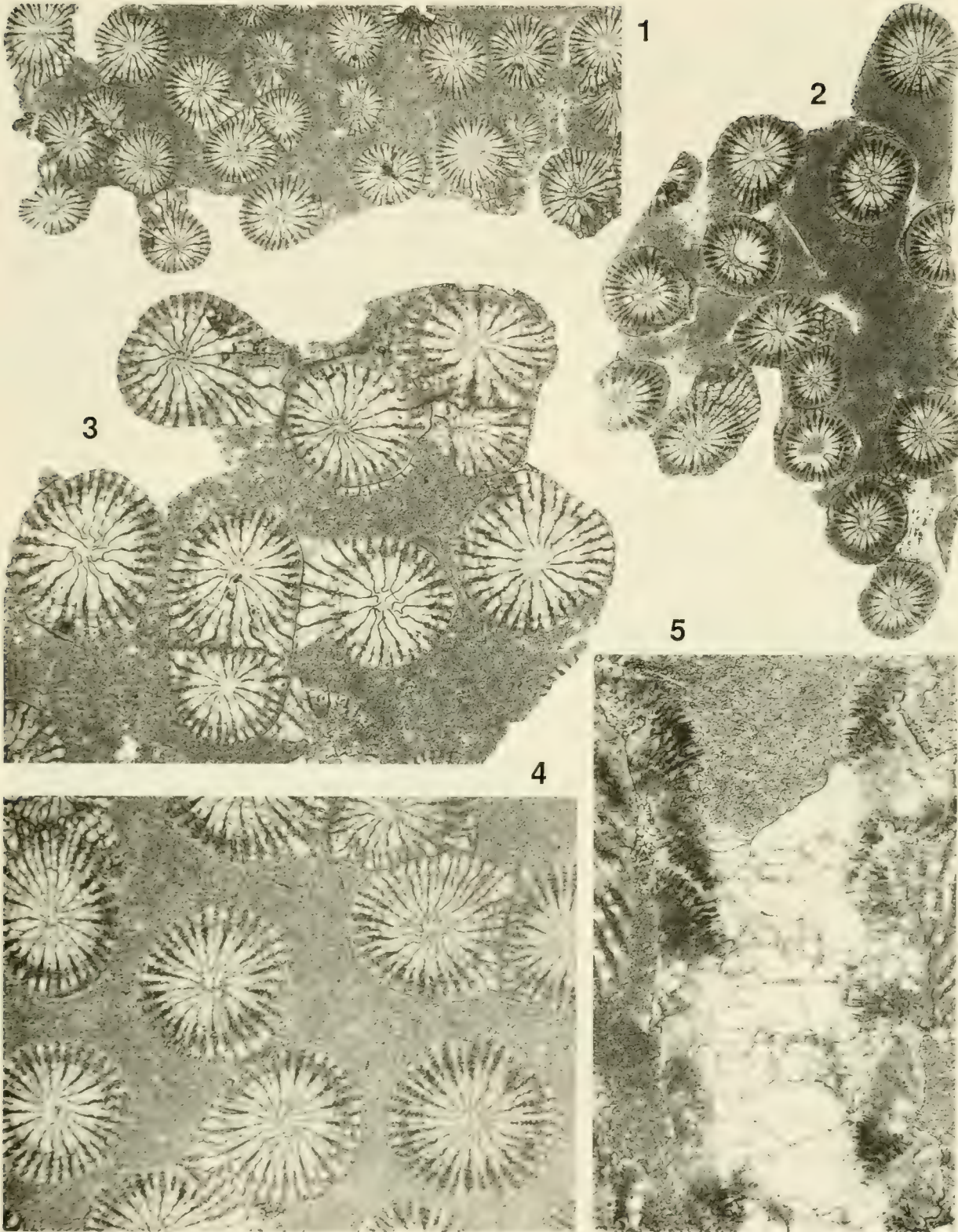


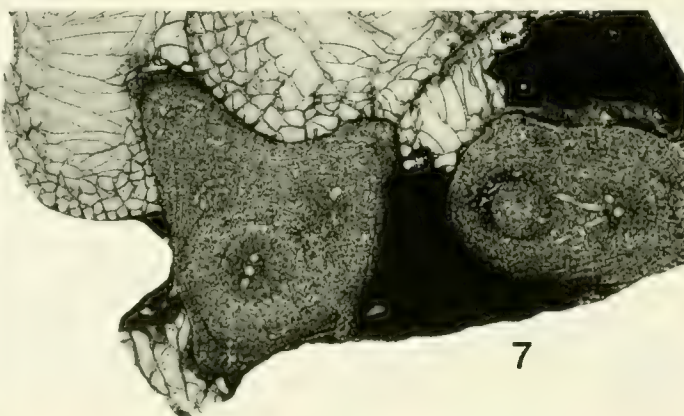
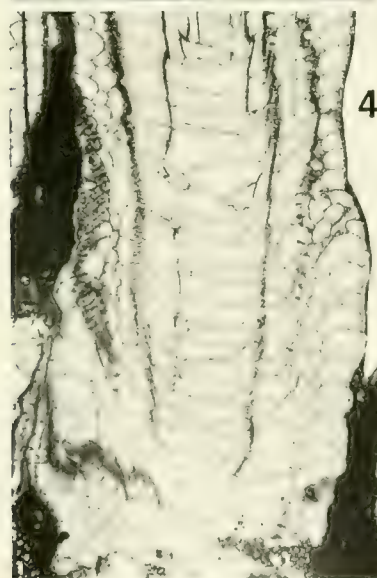
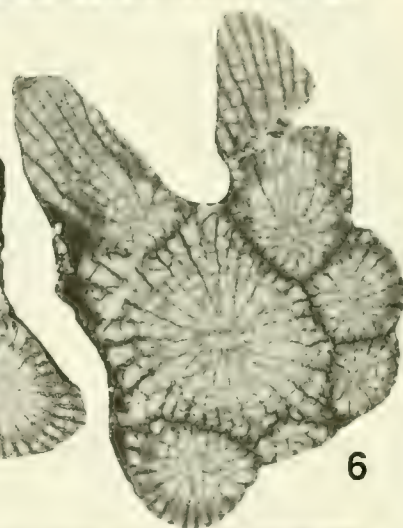
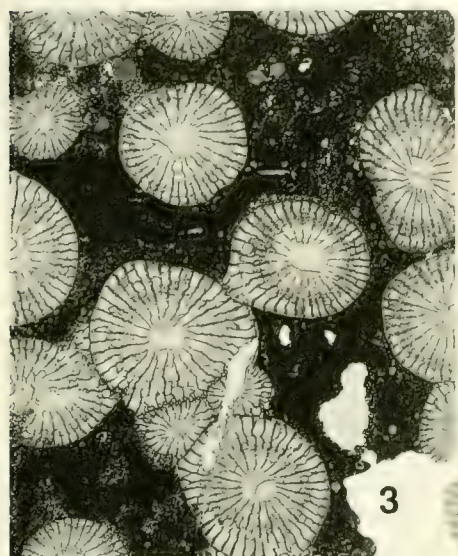
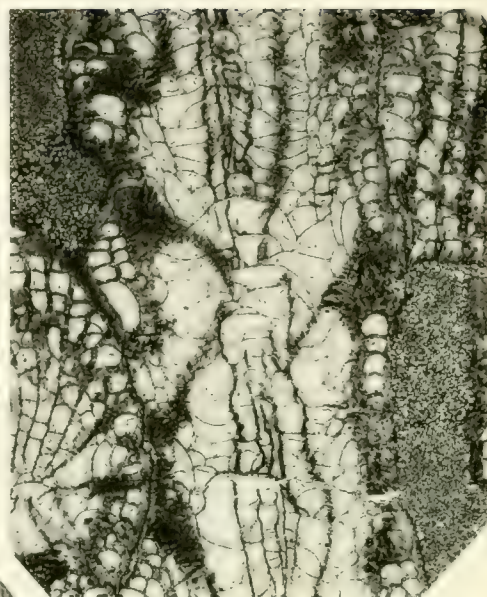
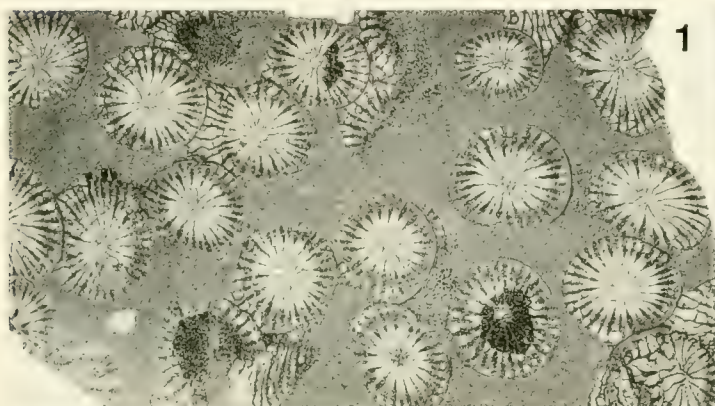
EXPLANATION OF PLATE 26

Figure	Page
1-2. <i>Characterophyllum nanum</i> (Hall and Whitfield, 1873)	54
1. P.R.I. 44750, longitudinal of corallite with abundant globose dissepiments and heavy dilation showing septal structure with typical bending of trabeculae, $\times 5$.	
2. P.R.I. 44751, transverse of individual with marked septal inflation in tabularium, (photographed from below), $\times 6.5$.	
3-10. <i>Disphyllum dispassum</i> (Fenton and Fenton, 1924)	58
3. F.M.N.H. 26045, holotype, transverse of corallite preparing to bud, $\times 3$.	
4. F.M.N.H. 26014, holotype of <i>Diphyphyllum tubiforme</i> , oblique, $\times 3$.	
5, 6. P.R.I. 44752, 5. transverse, showing variation in length of septa between corallites, $\times 3$; 6. longitudinal with wide dissepimentarium giving rise to bud, $\times 3$.	
7. P.R.I. 44753, transverse of corallite with long septa, $\times 3$.	
8. P.R.I. 44754, longitudinal, with prominent, widely spaced, complete tabulae, $\times 3$.	
9. P.R.I. 44755, transverse of long-septaed form with buds, $\times 3$.	
10. P.R.I. 44756, transverse, with buds, $\times 3$.	

EXPLANATION OF PLATE 27

Figure	Page
1-5. <i>Disphyllum floydense</i> (Belanski, 1928)	59
1, 3. U.S.N.M. 710296, paratype 1. transverse, $\times 2$; 3. enlargement of section to show corallites with typical septal dilation, $\times 4$.	
2. S.U.I. 364, transverse of specimen with heavily dilated septa, $\times 2$.	
4. P.R.I. 44757, transverse of corallites with long septa, some with lumpy trabeculae, $\times 4$.	
5. P.R.I. 44758, longitudinal of corallite with axially inclined thick septal trabeculae and with irregular tabulae, $\times 6$.	



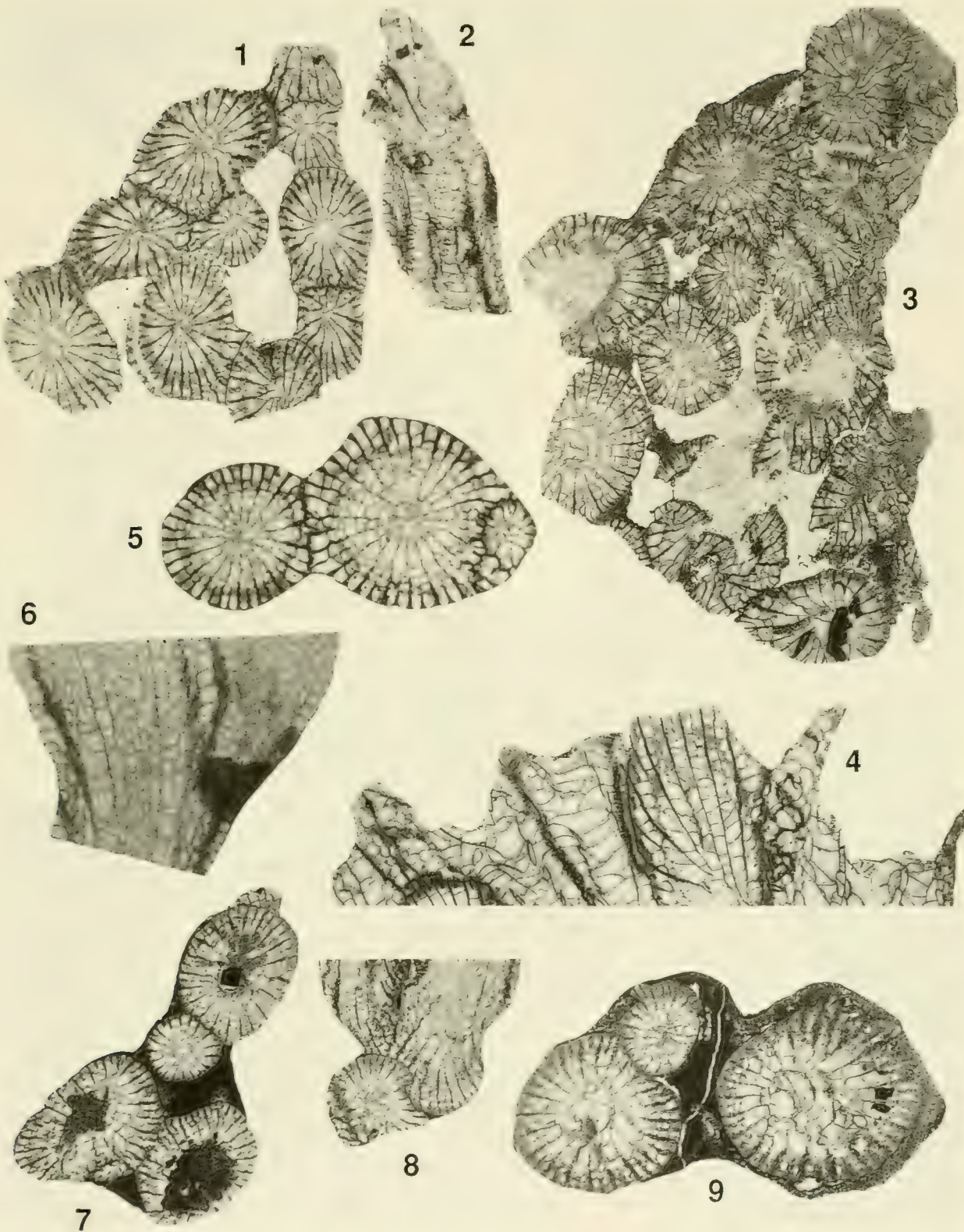


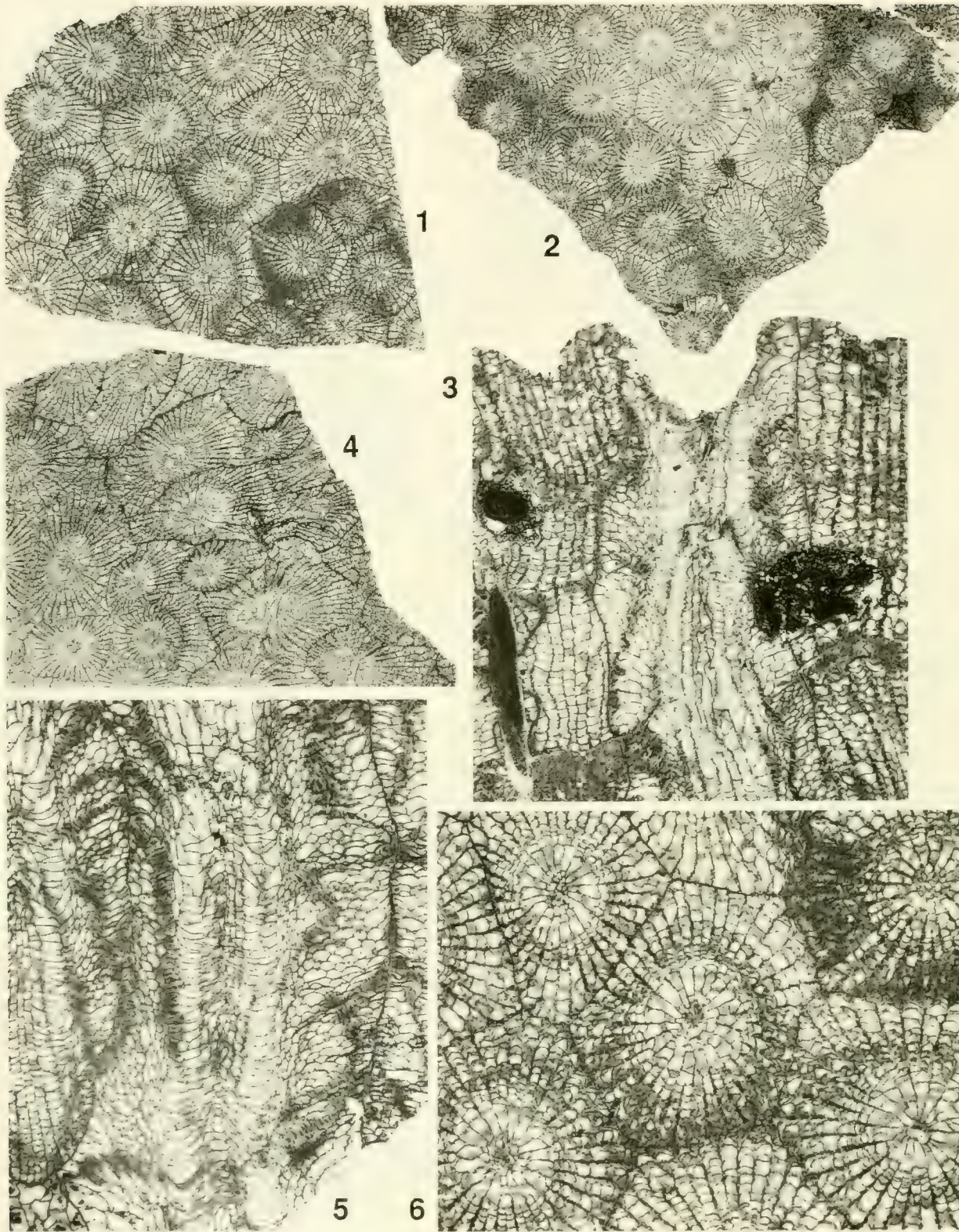
EXPLANATION OF PLATE 28

Figure	Page
1-4. <i>Disphyllum floydense</i> (Belanski, 1928)	59
1, 2. P.R.I. 44759; 1. transverse of typical colony, $\times 2$; 2. enlarged longitudinal illustrating variable development of dissepiments and bulbous peripheral dissepiments, $\times 6$.	
3, 4. P.R.I. 44760; 3. transverse of colony from southern (Marble Rock) area with large diameter corallites, $\times 2$; 4. longitudinal illustrating peripheral large dissepiments, $\times 4$.	
5-7. <i>Disphyllum conjugans</i> n. sp.	61
5, 6. S.U.I. 1625, holotype, 5. transverse, older; and 6. younger coralla with abundant budding, both $\times 5$.	
7. S.U.I. 1624, paratype, longitudinal, illustrating growth on fallen stromatoporoids, $\times 4$.	

EXPLANATION OF PLATE 29

Figure	Page
1-2. <i>Disphyllum conjugans</i> n. sp.	61
1, 2. S.U.I. 1376, paratype, 1. transverse of adult colony, $\times 3$; 2. longitudinal, with outer row of large dissepiments, $\times 3$.	
3-9. <i>Disphyllum iowensis</i> n. sp.	62
3, 4. S.U.I. 541, holotype, 3. transverse, with variable septa, partly crushed, $\times 2$; 4. longitudinal, with calicinal pit, $\times 3$.	
5, 6. S.U.I. 1626, paratype, 5. transverse, with long septa, $\times 5$; 6. longitudinal, with large outer dissepiments, $\times 5$.	
7, 8. S.U.I. 1756, paratype, 7. transverse, with thin septa and open axial space, $\times 2$; 8. partly longitudinal, $\times 2$.	
9. S.U.I. 1509, paratype, transverse, with open axial space and heavy septa at wall, $\times 3$.	



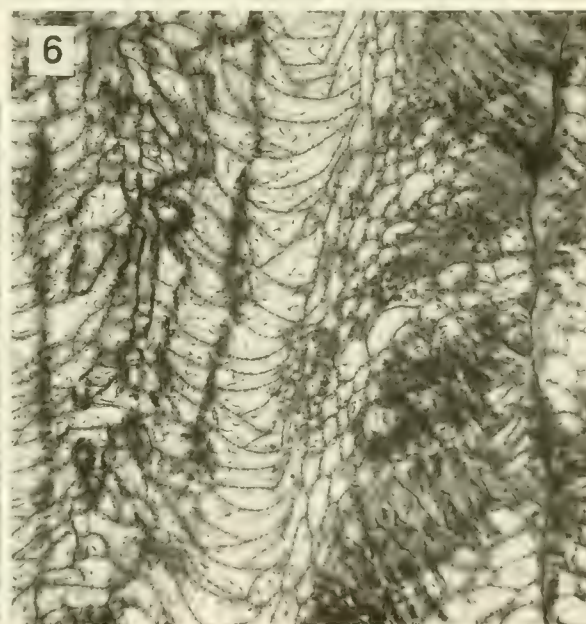
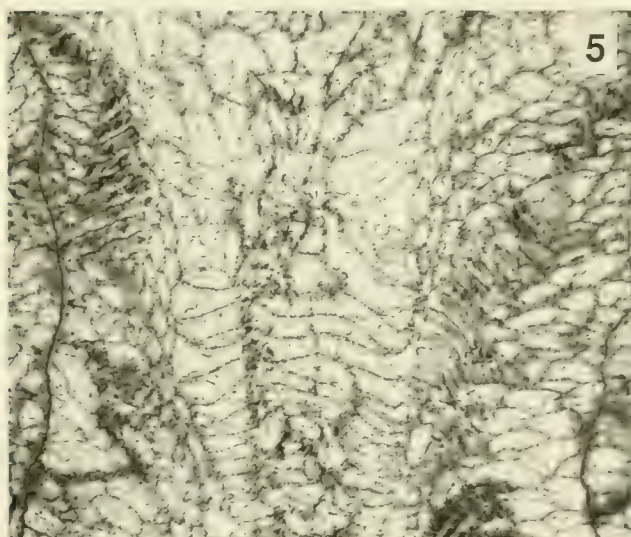
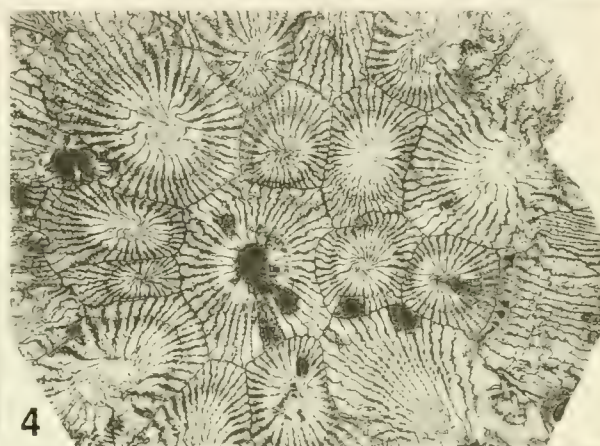
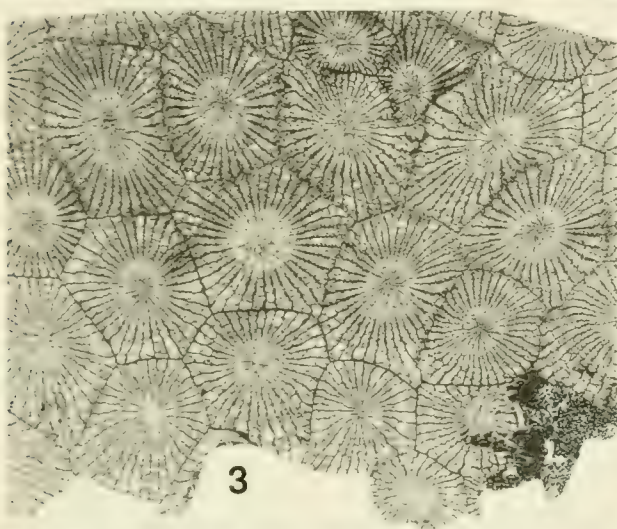
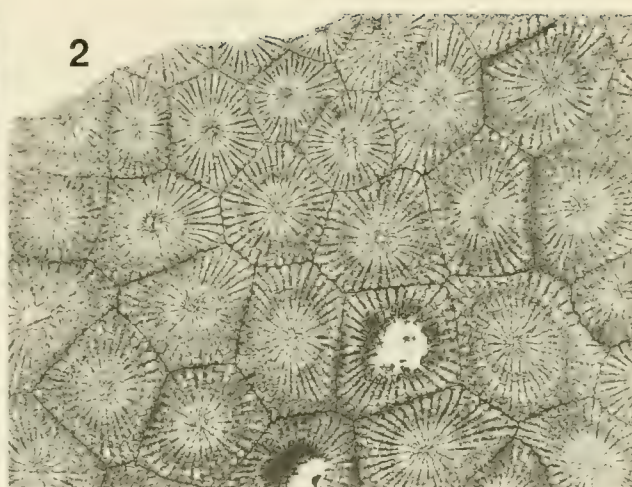
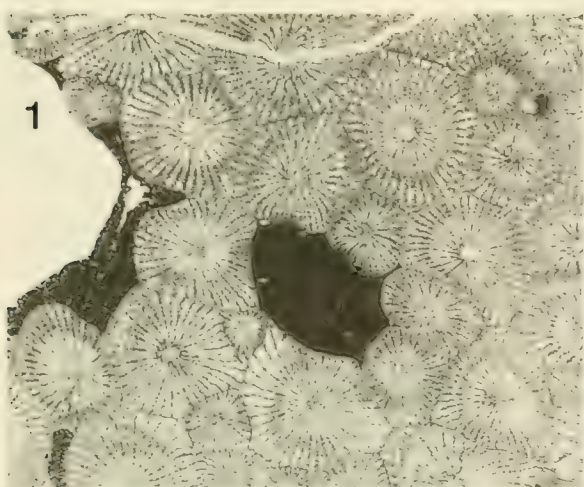


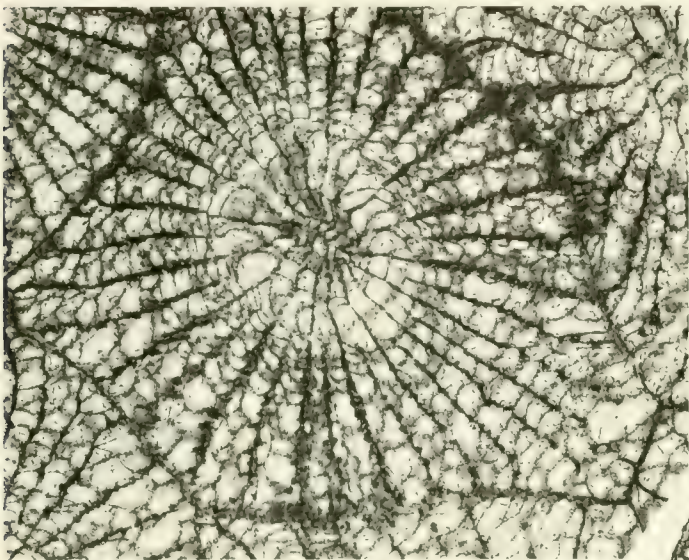
EXPLANATION OF PLATE 30

Figure	Page
1-6. <i>Hexagonaria bassleri</i> (Webster and Fenton, 1924)	64
1. U.S.N.M. 78619, holotype— <i>H. bassleri bassleri</i> , transverse of colony, $\times 2$.	
2, 3. U.S.N.M. 78620, holotype— <i>H. bassleri depressa</i> , 1. transverse, showing smallish corallites, $\times 2$; 2. longitudinal of corallite with calicinal pit, $\times 5$.	
4. U.S.N.M. 78621, paratype, <i>H. bassleri bassleri</i> , transverse, $\times 2$.	
5, 6. U.S.N.M. 78619, holotype of <i>H. bassleri</i> , 5. longitudinal, illustrating axial and periaxial tabulae as well as broad dissepimentarium with numerous dissepiments, $\times 5$; 6. transverse, with varied septal dilation, $\times 5$.	

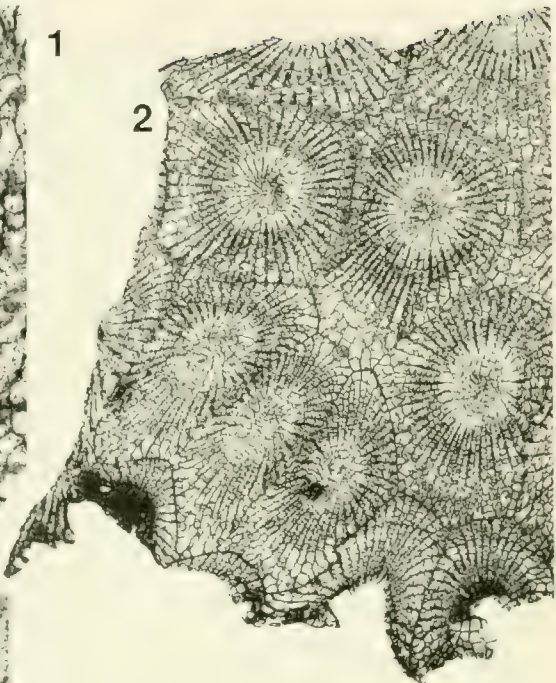
EXPLANATION OF PLATE 31

Figure	Page
1-6. <i>Hexagonaria bassleri</i> (Webster and Fenton, 1924)	64
1. P.R.I. 44761, transverse of colony with variable development of inflated septa trabeculae, $\times 2$.	
2. P.R.I. 44762, transverse of colony with dilated septa, $\times 2$.	
3. P.R.I. 44763, transverse, showing variable development of carinae-like structures in dilated septa, $\times 2$.	
4. U.M.M.P. 8085, paratype of <i>H. bassleri</i> , transverse, with "spindle-shaped" septal dilation, $\times 2$.	
5. P.R.I. 44764, longitudinal, to illustrate tabularium with axial and periaxial rows of tabulae and septal structure of inclined monacanthine trabeculae, $\times 10$.	
6. P.R.I. 44762, longitudinal of dissepimentarium and inclined monacanthine septal trabeculae, $\times 10$.	





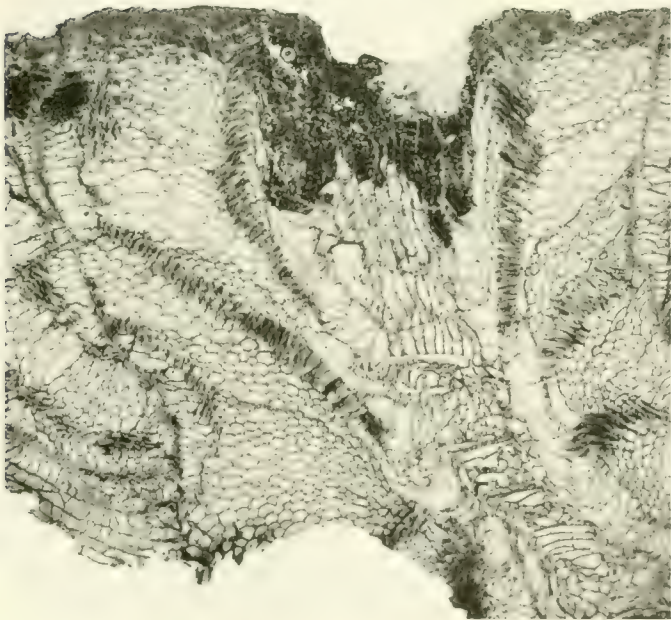
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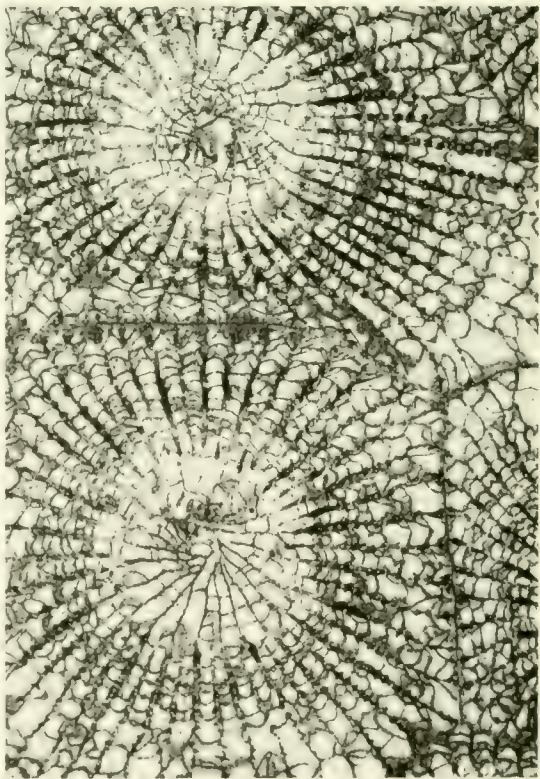
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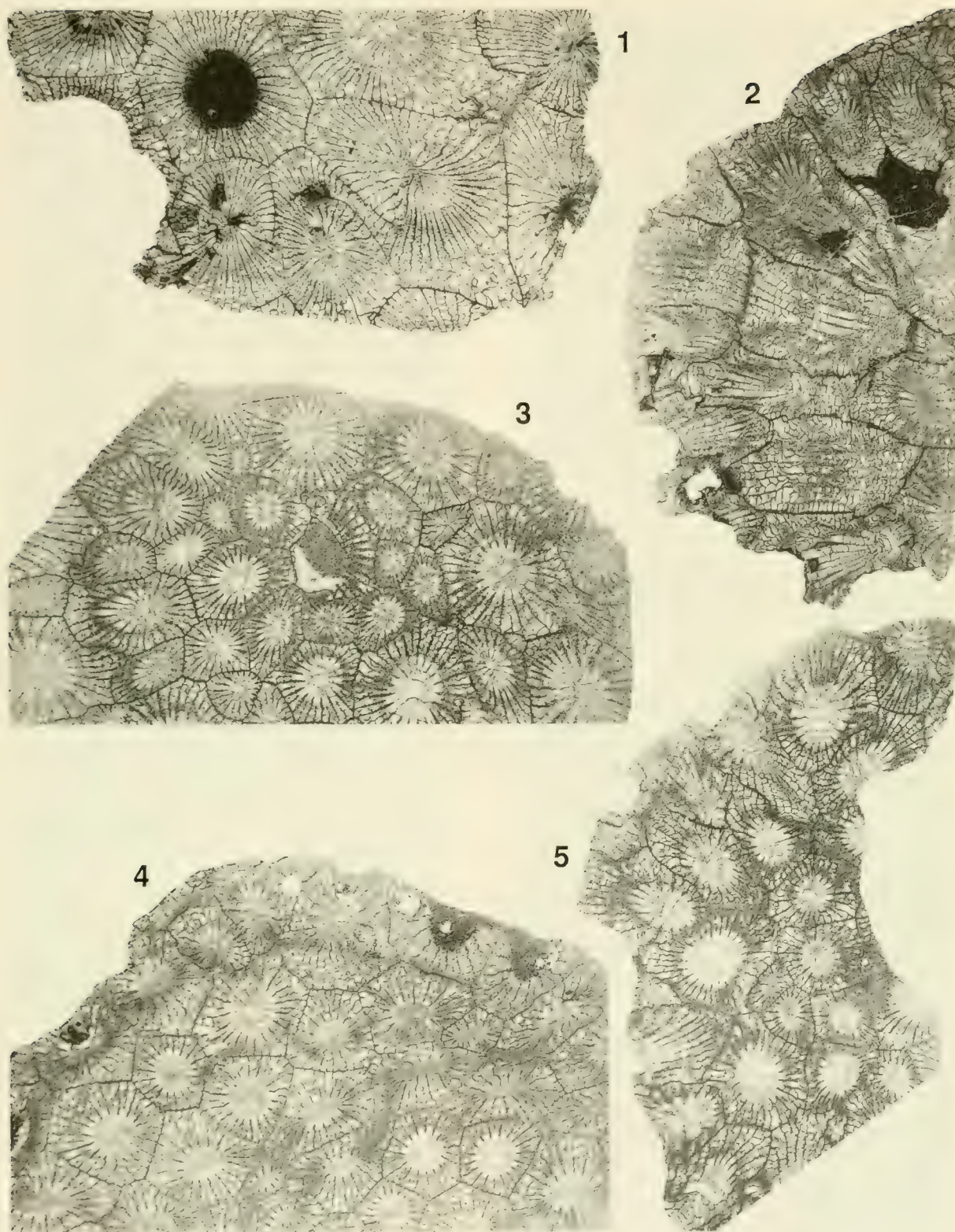
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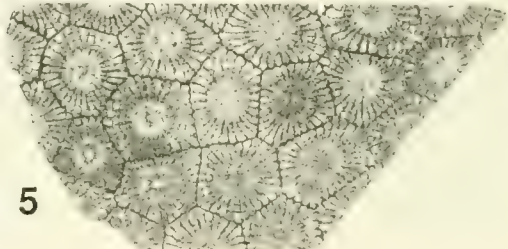
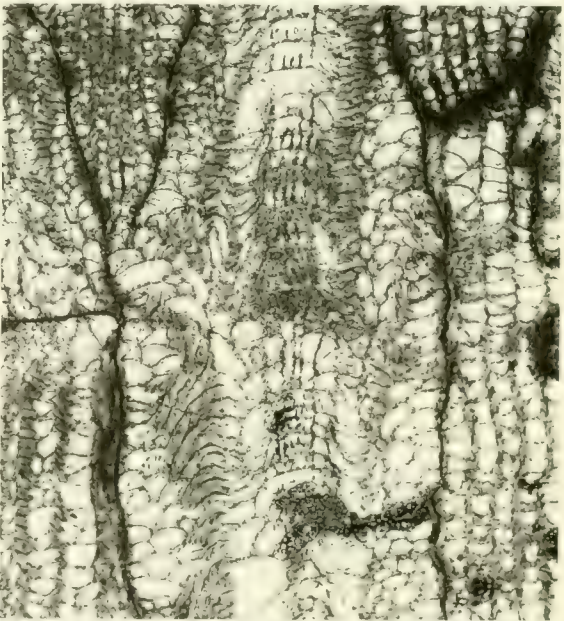
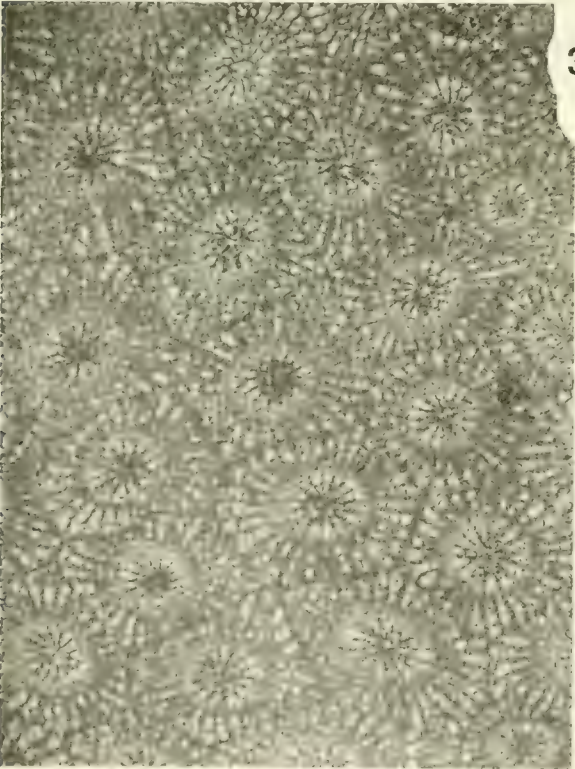
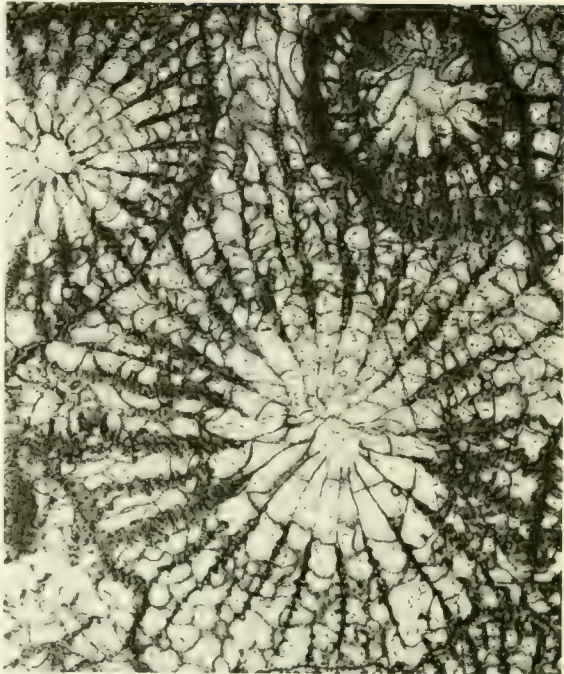
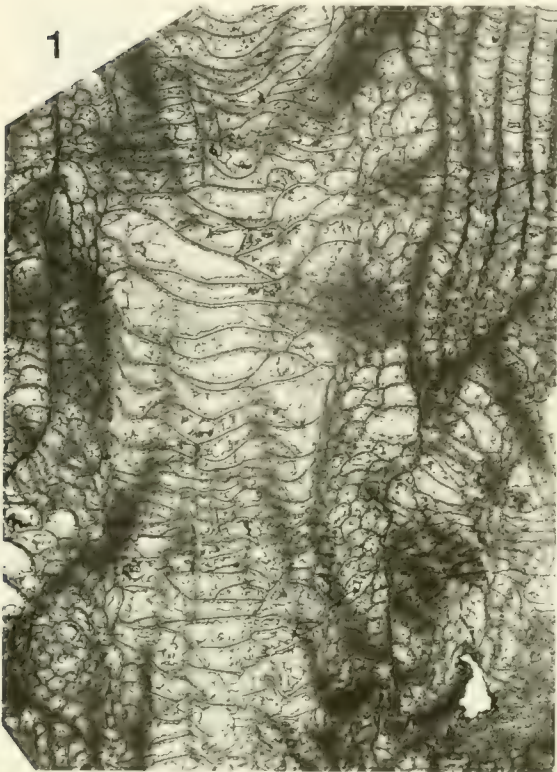
EXPLANATION OF PLATE 32

Figure	Page
1. <i>Hexagonaria bassleri</i> (Webster and Fenton, 1924)	64
1. P.R.I. 44763, transverse, enlarged to illustrate incomplete septa and enlarged dissepiments prior to budding (arrow) and carinae-like structures in septa resulting from enlarge septal trabeculae, $\times 8$.	
2-5. <i>Hexagonaria bassleri magna</i> (Webster and Fenton, 1924)	67
2-5. U.S.N.M. 78637, holotype of <i>H. bassleri magna</i> , 2. transverse of colony with very large corallites and variable but heavy septal dilation, $\times 2$; 3. longitudinal, $\times 2$; 4. longitudinal, enlargement of single corallite to illustrate tabulae, septal structure, and broad dissepimentarium with banding evident, $\times 4$; 5. transverse of large corallites and "carination" of septa, $\times 5$.	

EXPLANATION OF PLATE 33

Figure	Page
1. <i>Hexagonaria bassleri magna</i> (Webster and Fenton, 1924)	67
1. U.S.N.M. 335007, transverse of colony with typically large corallites, $\times 2$.	
2-5. <i>Hexagonaria oweni</i> (Belanski, 1928)	67
2. S.U.I. 471, holotype, transverse and oblique, $\times 2$.	
3. P.R.I. 44766, transverse of typical colony with septal dilation in inner dissepimentarium, $\times 2$.	
4. P.R.I. 44767, transverse of colony with light skeleton, $\times 2$.	
5. P.R.I. 44768, transverse of colony with local heavy dilation of septa and walls, $\times 2$.	



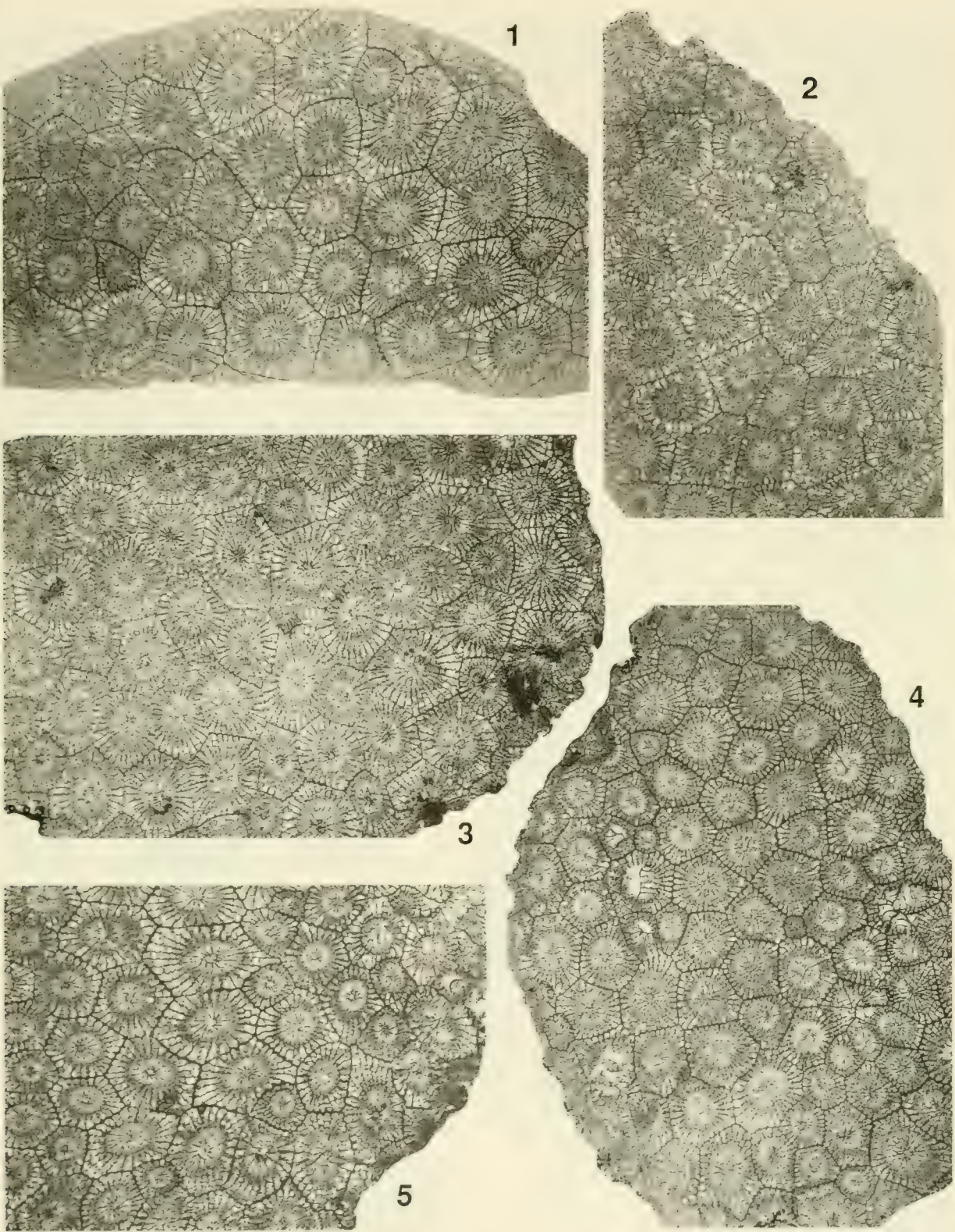


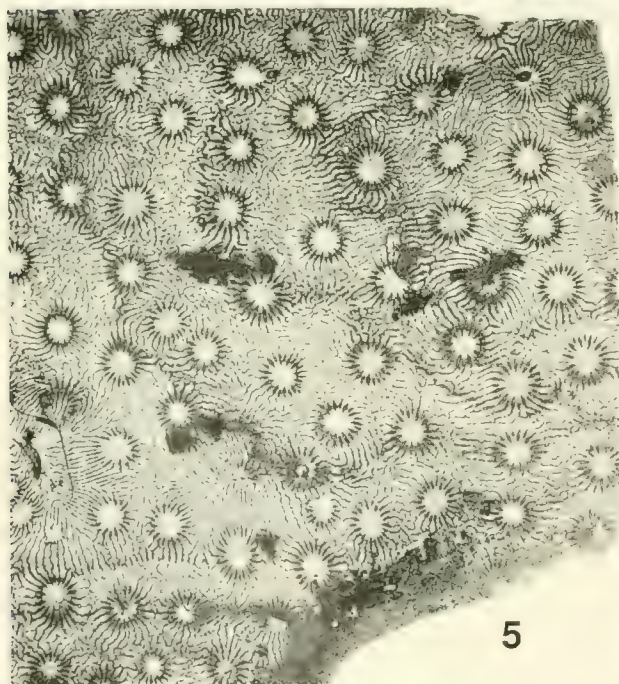
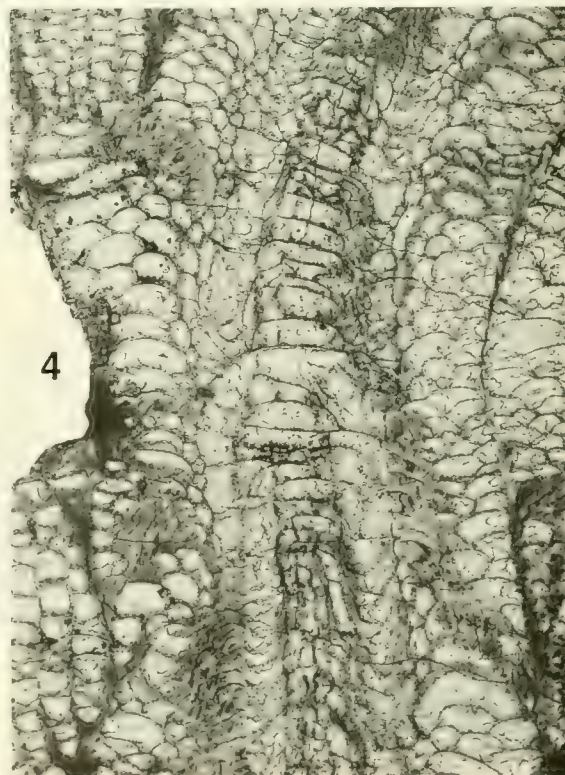
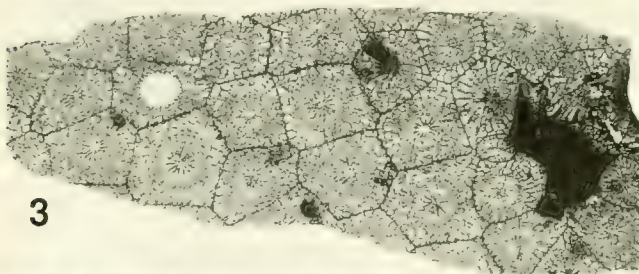
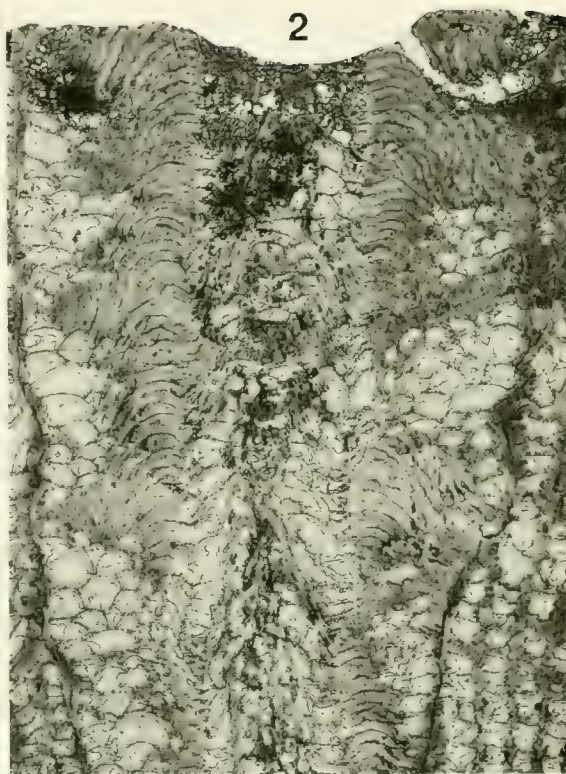
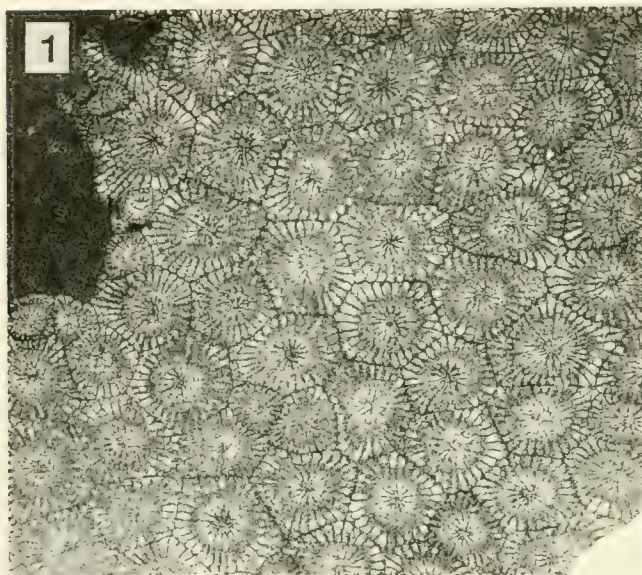
EXPLANATION OF PLATE 34

Figure	Page
1, 2. <i>Hexagonaria oweni</i> (Belanski, 1928)	67
1. U.S.N.M. 71041, paratype, longitudinal of corallite with typical tabularium and numerous dissepiments, $\times 6$.	
2. P.R.I. 44769, transverse, enlarged to illustrate swollen septal trabeculae and "carinae", $\times 6$.	
3-5. <i>Hexagonaria inequalis</i> (Hall and Whitfield, 1873)	68
3. N.Y.S.M. 3000/1, holotype of <i>H. inequalis</i> , transverse of specimen with small corallites and considerable septal dilation throughout, $\times 5$.	
4, 5. U.S.N.M. 78635, Fenton and Fenton illustrated specimen (1924, Pl. 14, fig. 7), 4. longitudinal of corallite with typically incurved septal trabeculae and axial and periaxial rows of tabulae, $\times 7$; 5. transverse of corallum, $\times 2$.	

EXPLANATION OF PLATE 35

Figure	Page
1-5. <i>Hexagonaria inequalis</i> (Hall and Whitfield, 1873)	68
1. U.M.M.P. 5319, holotype, <i>H. whitfieldi</i> , transverse of colony with broad dissepimentarium and elongate septa, $\times 2$.	
2. E.M.N.H. 26055, paratype, <i>H. whitfieldi</i> , transverse of colony with narrow dissepimentarium, $\times 2$.	
3. P.R.I. 44770, transverse of large diameter specimen, $\times 2$.	
4. P.R.I. 44771, transverse, showing corallites with narrow dissepimentarium, $\times 2$.	
5. P.R.I. 44772, transverse of small diameter specimen with dissepimentarium of variable width, $\times 2$.	



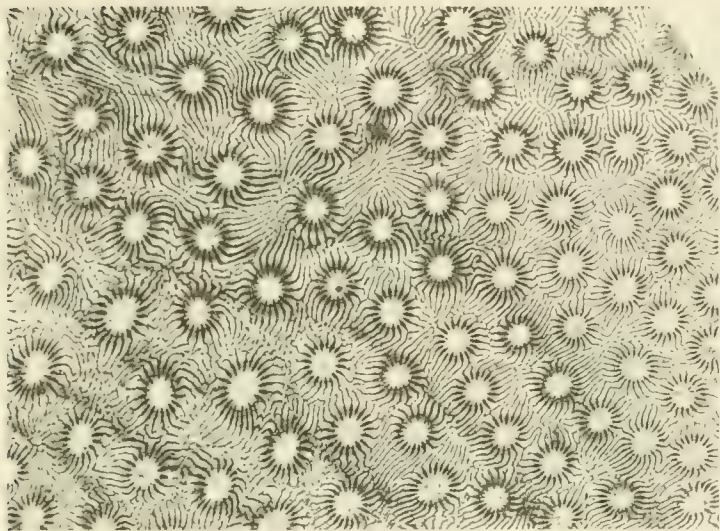


EXPLANATION OF PLATE 36

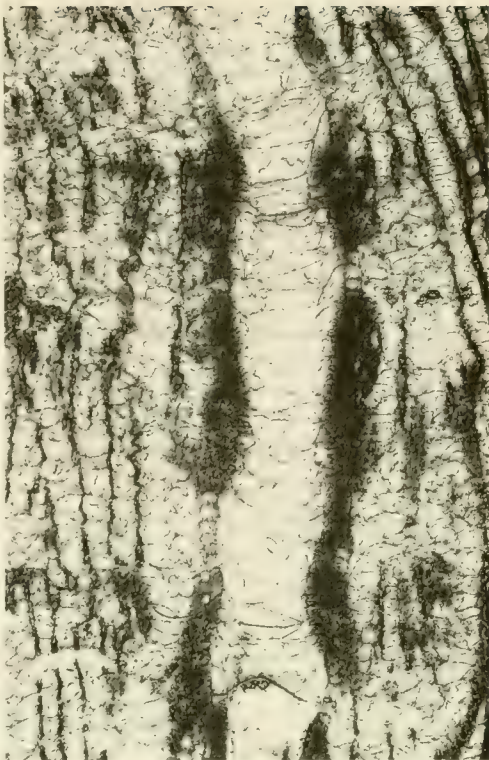
Figure	Page
1-4. <i>Hexagonaria inequalis</i> (Hall and Whitfield, 1873)	68
1. P.R.I. 44773, transverse of corallum with small diameter corallites, $\times 2$.	
2. P.R.I. 44774, longitudinal, showing characteristic inbending of monacanthine septal trabeculae, $\times 9$.	
3. F.M.N.H. 26048, Webster and Fenton "Plesiotype" of <i>H. inequalis</i> , transverse of small colony resembling holotype of <i>H. inequalis</i> , $\times 2$.	
4. P.R.I. 44775, longitudinal, with characteristic axial and periaxial rows of tabulae, $\times 9$.	
5. <i>Pachyphyllum minutissimum</i> Webster, 1905	73
5. U.S.N.M. 78648, holotype, transverse of corallum with small corallites and marked septal dilation at outer border of tabularium, $\times 2$.	

EXPLANATION OF PLATE 37

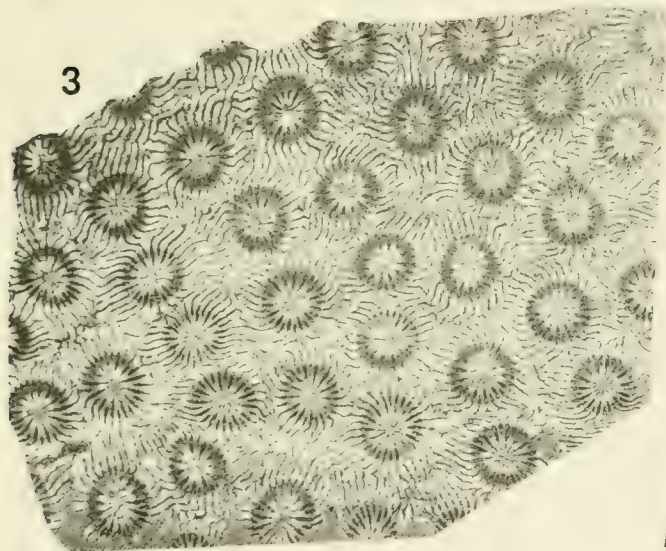
Figure	Page
1-6. <i>Pachyphyllum minutissimum</i> Webster, 1905	73
1. P.R.I. 44776, transverse of colony with very small diameter corallites, $\times 2$.	
2. U.S.N.M. 78624, holotype, longitudinal, with typical complete tabulae and horseshoe dissepiments, $\times 7$.	
3. P.R.I. 44777, transverse, corallites with large diameter, $\times 2$.	
4. P.R.I. 44778, transverse, small colony with strong septal dilation, $\times 2$.	
5. P.R.I. 44779, transverse, small diameter corallites with heavy dilation and long septa, corallites aphroid in part, $\times 2$.	



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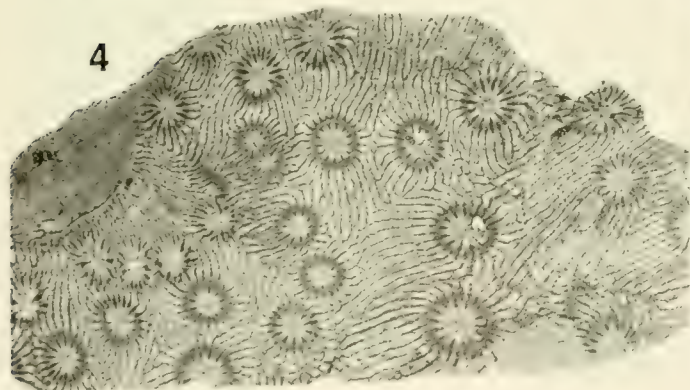
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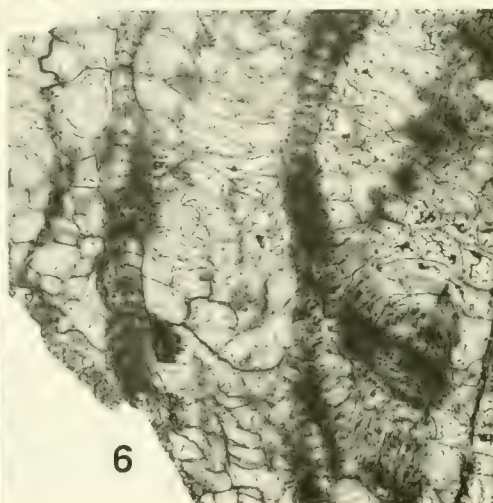
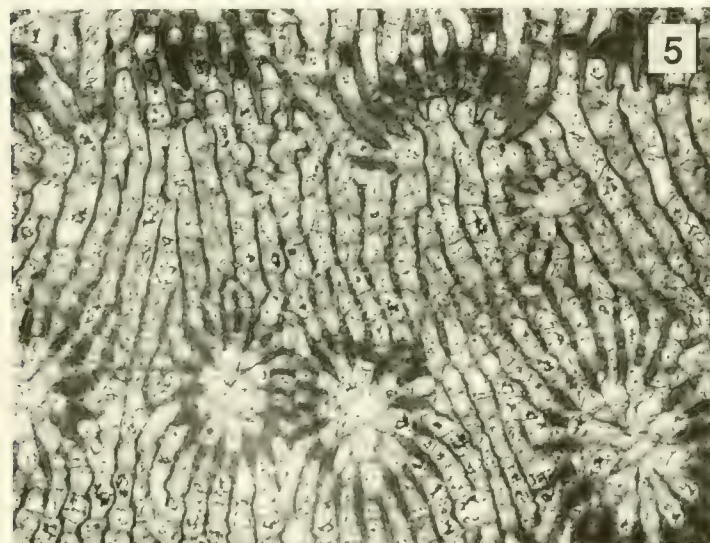
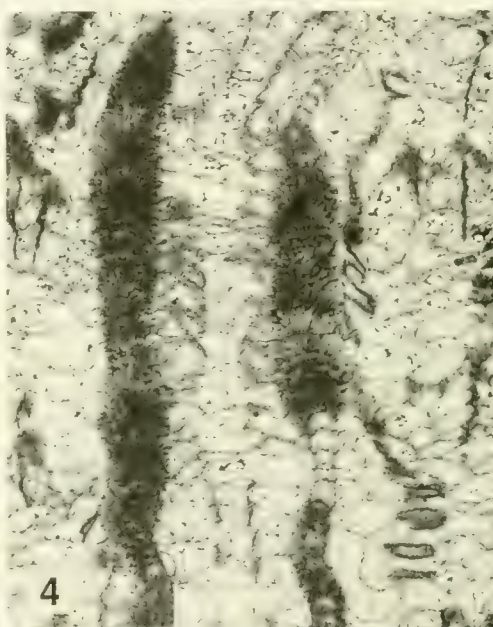
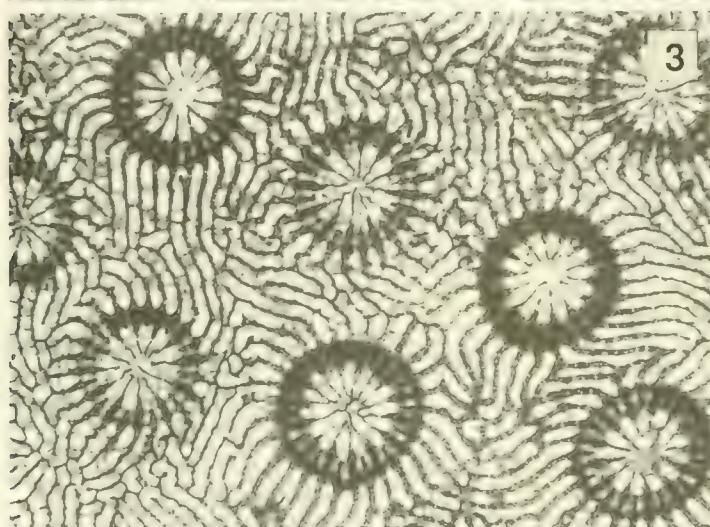
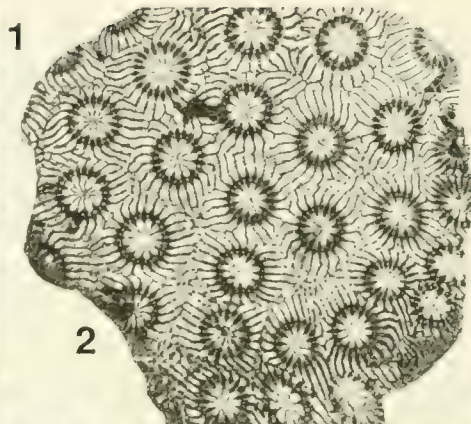
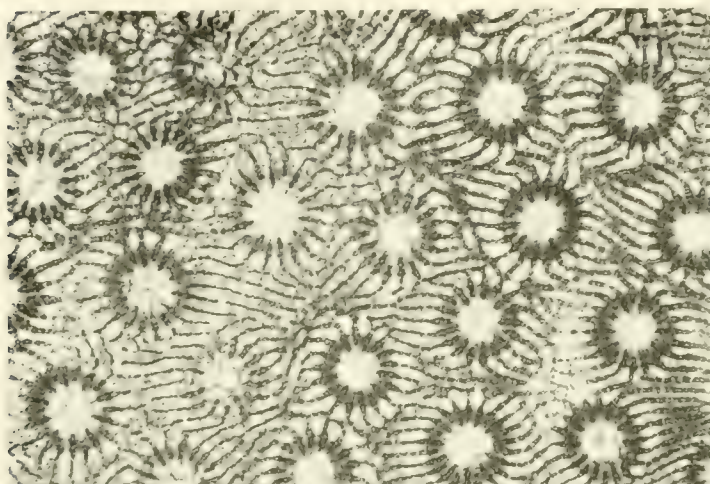
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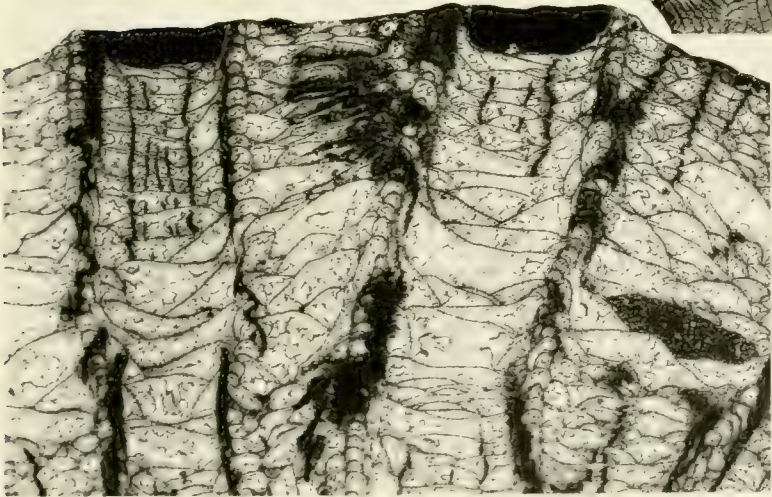
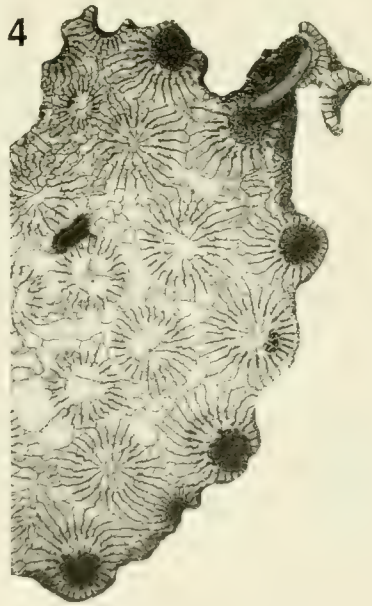
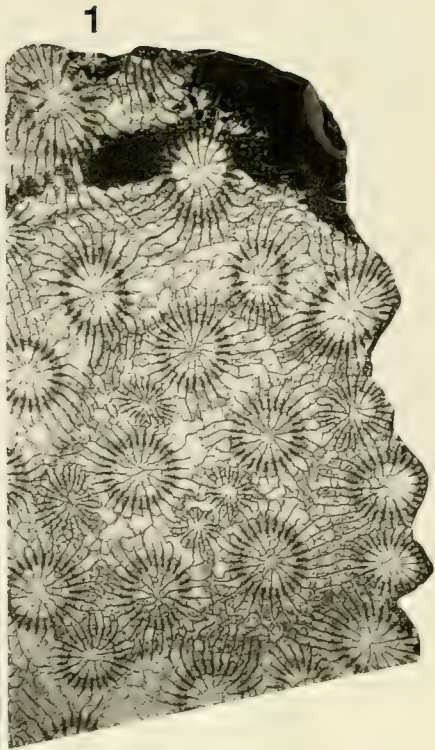
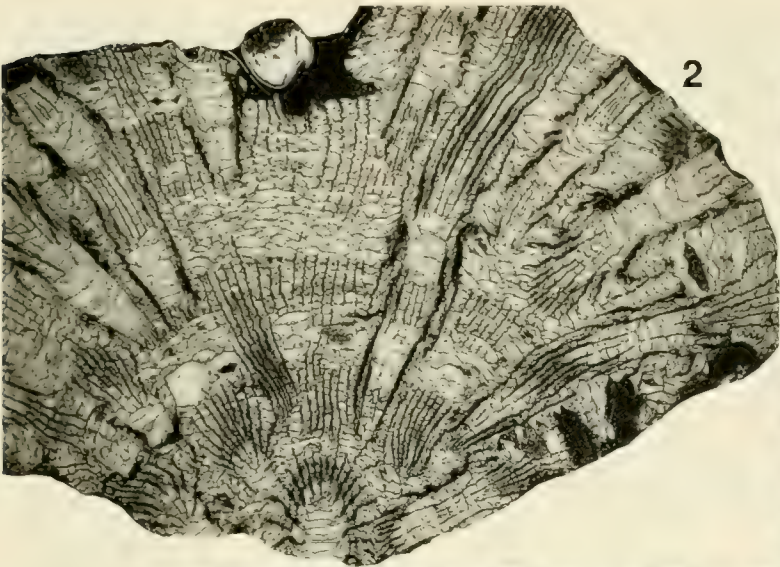
EXPLANATION OF PLATE 38

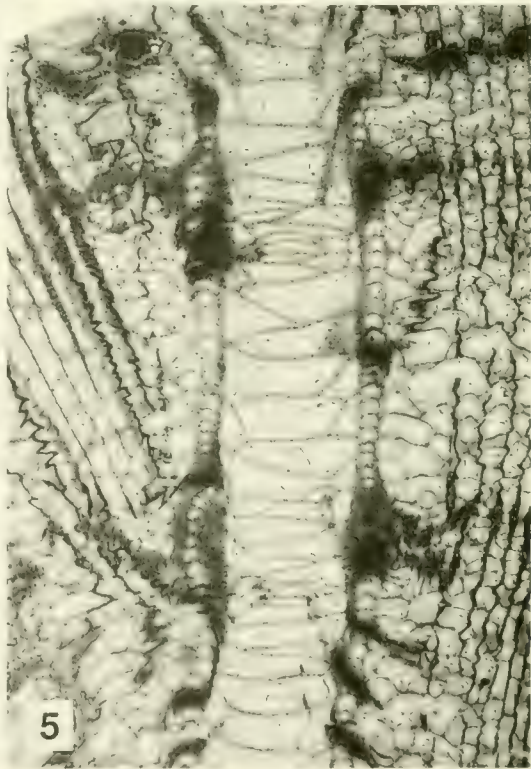
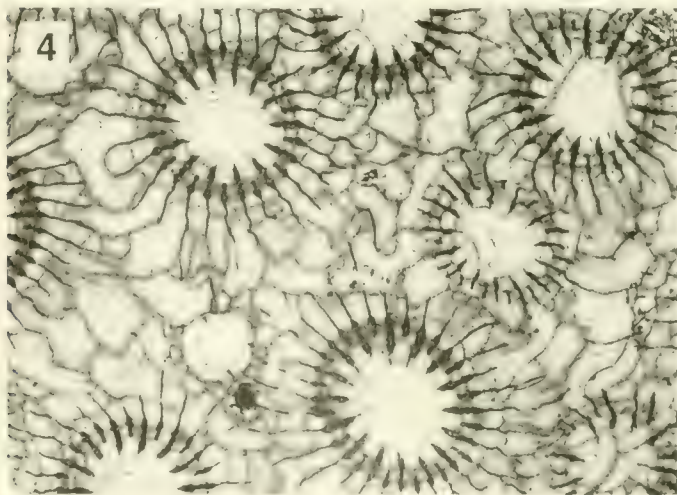
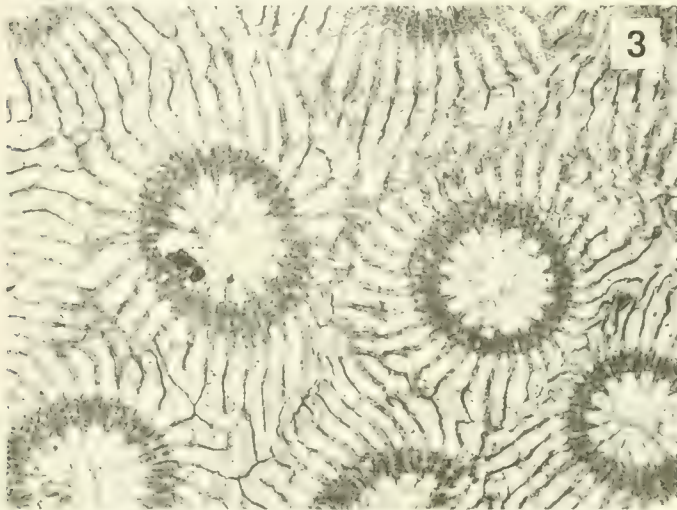
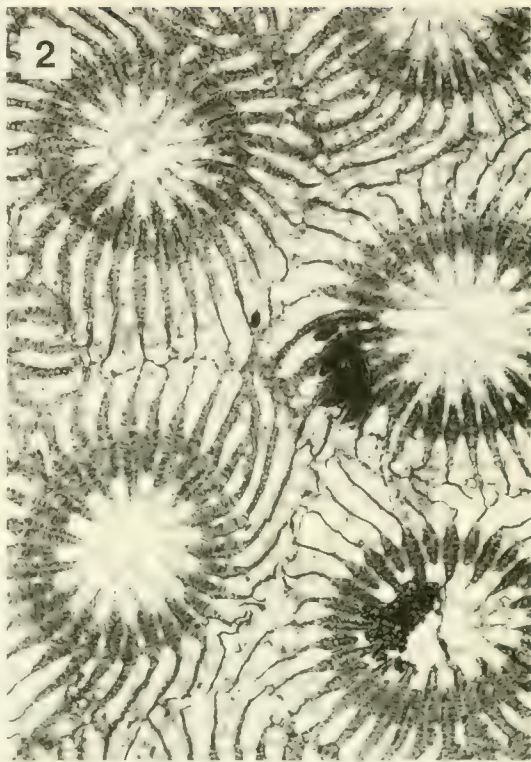
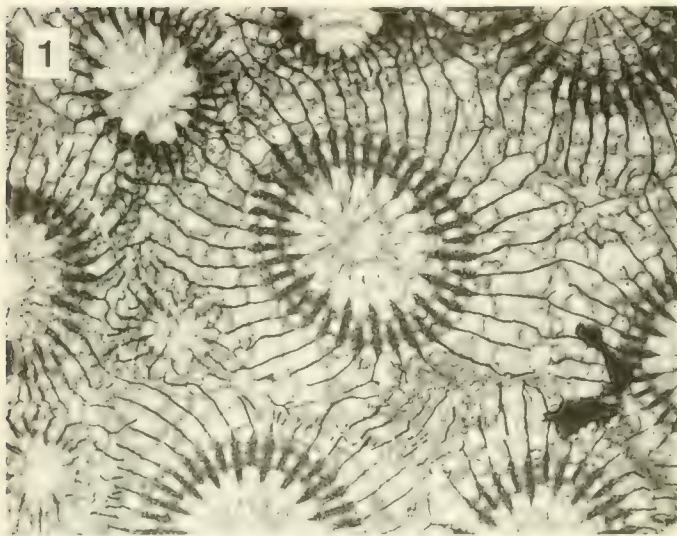
Figure	Page
1-6. <i>Pachyphyllum minutissimum</i> Webster, 1905	73
1. P.R.I. 44780, transverse of small diameter corallites with marked dilation of septa, $\times 5$.	
2. P.R.I. 44781, transverse of typical small colony from Nora Springs Dam, $\times 2$.	
3. P.R.I. 44782, transverse of large corallites with some confluency between individuals, $\times 5$.	
4. P.R.I. 44783, longitudinal, enlarged to show horseshoe dissepiments and fans of septal trabeculae, $\times 8$.	
5. P.R.I. 44784, transverse, illustrating budding in colony, $\times 8$.	
6. P.R.I. 44781, longitudinal, illustrating horseshoe dissepiments and septal structure in dissepimentarium, $\times 9$.	

7

EXPLANATION OF PLATE 39

Figure	Page
1-5. <i>Pachyphyllum gregarium</i> Webster, 1905	75
1, 2. U.S.N.M. 78645, lectotype, 1. longitudinal, with seasonal(?) banding shown by size of dissepiments and spacing of tabulae, $\times 2$; 2. transverse illustrating slightly aphroid nature of corallites, $\times 2$.	
3, 4. U.S.N.M. 78645A, lectoparatype, 3. longitudinal, with complete, flattish tabulae, $\times 2$; 4. transverse of colony with aphroid corallites in center. $\times 2$.	
5. U.S.N.M. 78645, longitudinal of portion of lectotype showing typical tabularium and somewhat irregular development of row of horseshoe dissepiments, $\times 6$.	



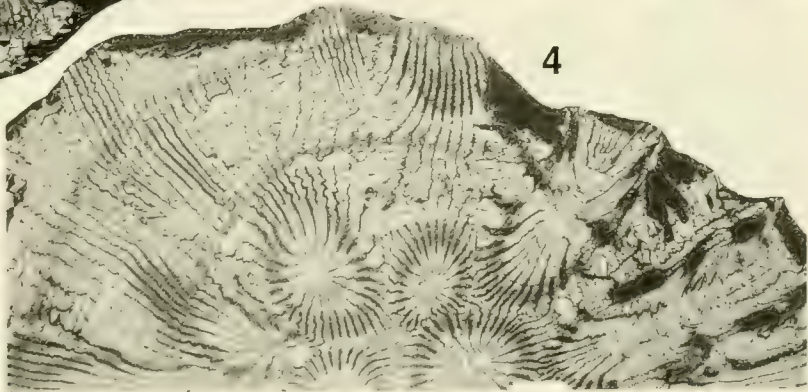
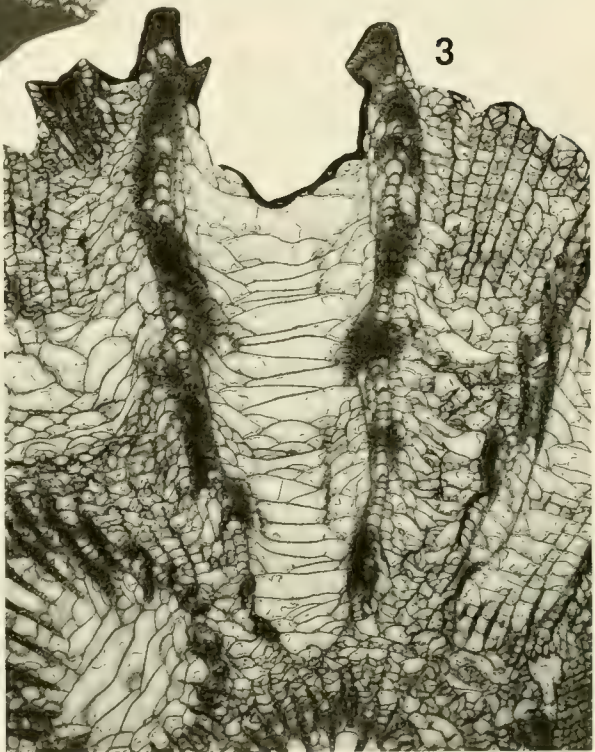
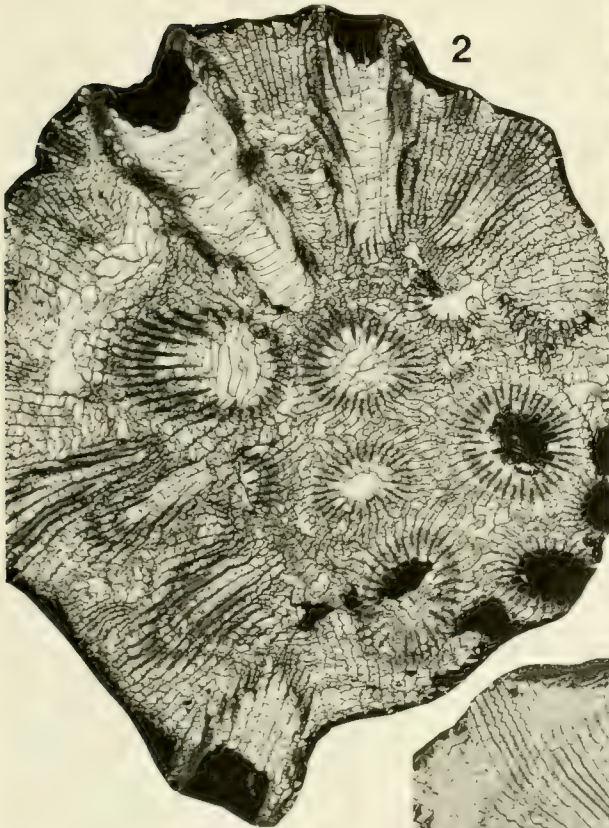


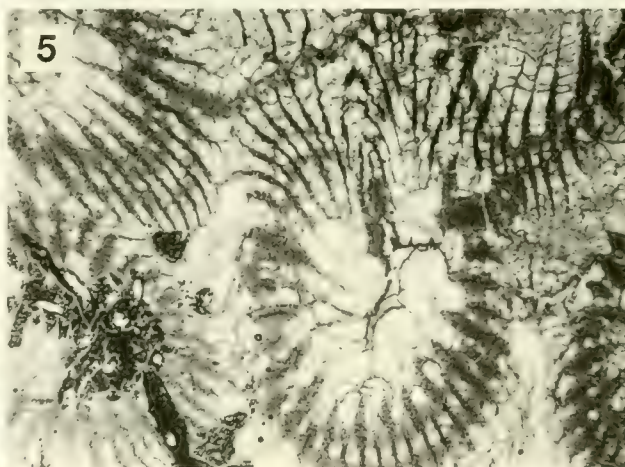
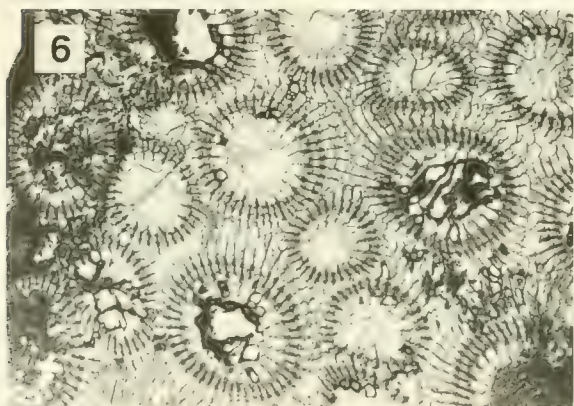
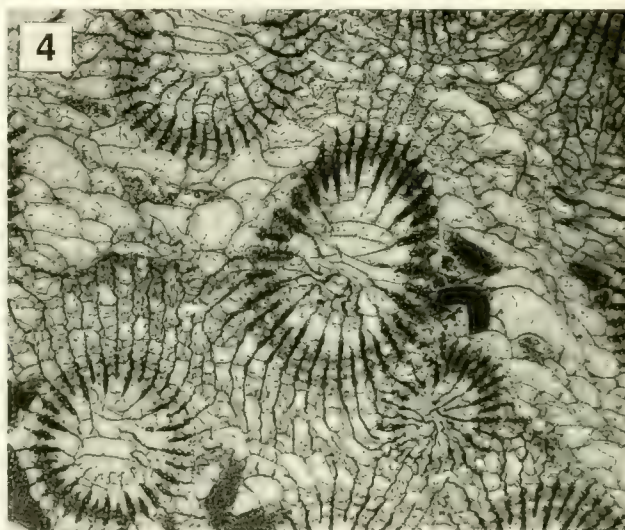
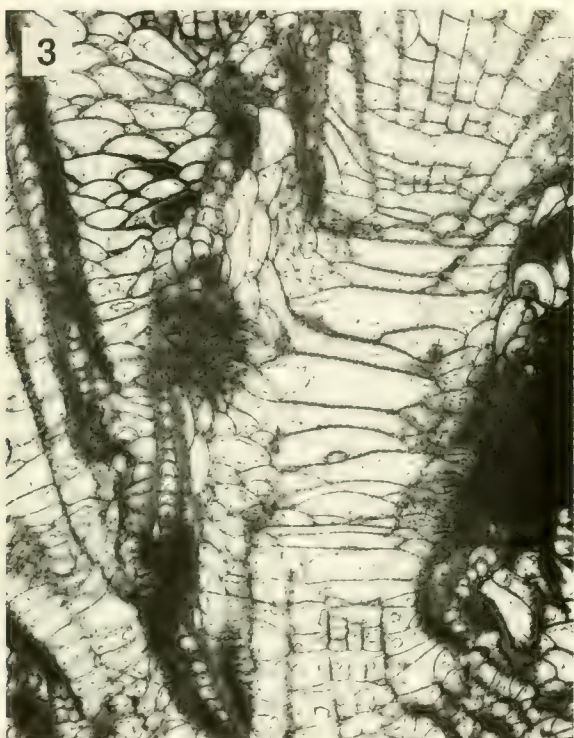
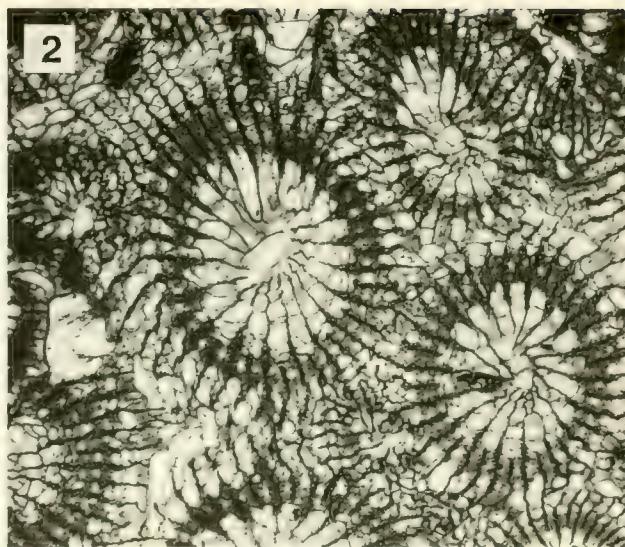
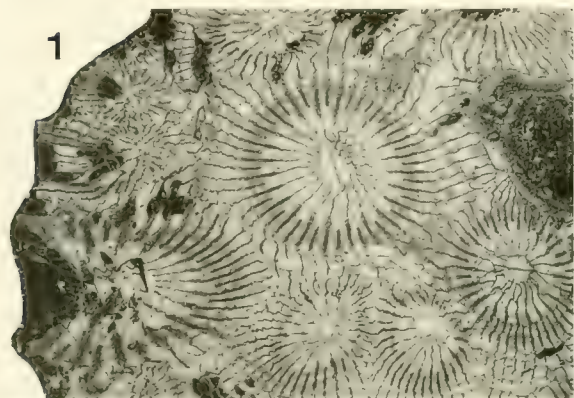
EXPLANATION OF PLATE 40

Figure	Page
1-5. <i>Pachyphyllum gregarium</i> Webster, 1905	75
1. P.R.I. 44786, transverse, corallites with dilation of septa over uniform collar of horseshoe dissepiments, $\times 5$.	
2. P.R.I. 44787, transverse, corallites with heavy dilation of septa and indistinct walls between individuals, $\times 5$.	
3. P.R.I. 44788, transverse of dilated form, $\times 5$.	
4. P.R.I. 44789, transverse of individuals with light dilation of septa and aphroid nature of colony, $\times 5$.	
5. P.R.I. 44790, longitudinal, corallite with uniform horseshoe dissepiments, no internal dissepiments, and complete tabulae, $\times 5$.	

EXPLANATION OF PLATE 41

Figure	Page
1-4. <i>Pachyphyllum websteri</i> Belanski, 1928	76
1. S.U.I. 2176, holotype, longitudinal, illustrating tabulae and large, irregular dissepiments in large corallites, $\times 2$.	
2, 3. U.S.N.M. 71030, paratype, 2. transverse and longitudinal of colony with rapidly diverging corallites, with occasional occurrence of large, irregular dissepiments, $\times 2$; 3. longitudinal, enlargement with typically irregular tabulae, horseshoe dissepiments and varied outer dissepimentarium, $\times 4$.	
4. S.U.I. 729, paratype, transverse with longitudinal sections of rapidly diverging corallites, $\times 2$.	



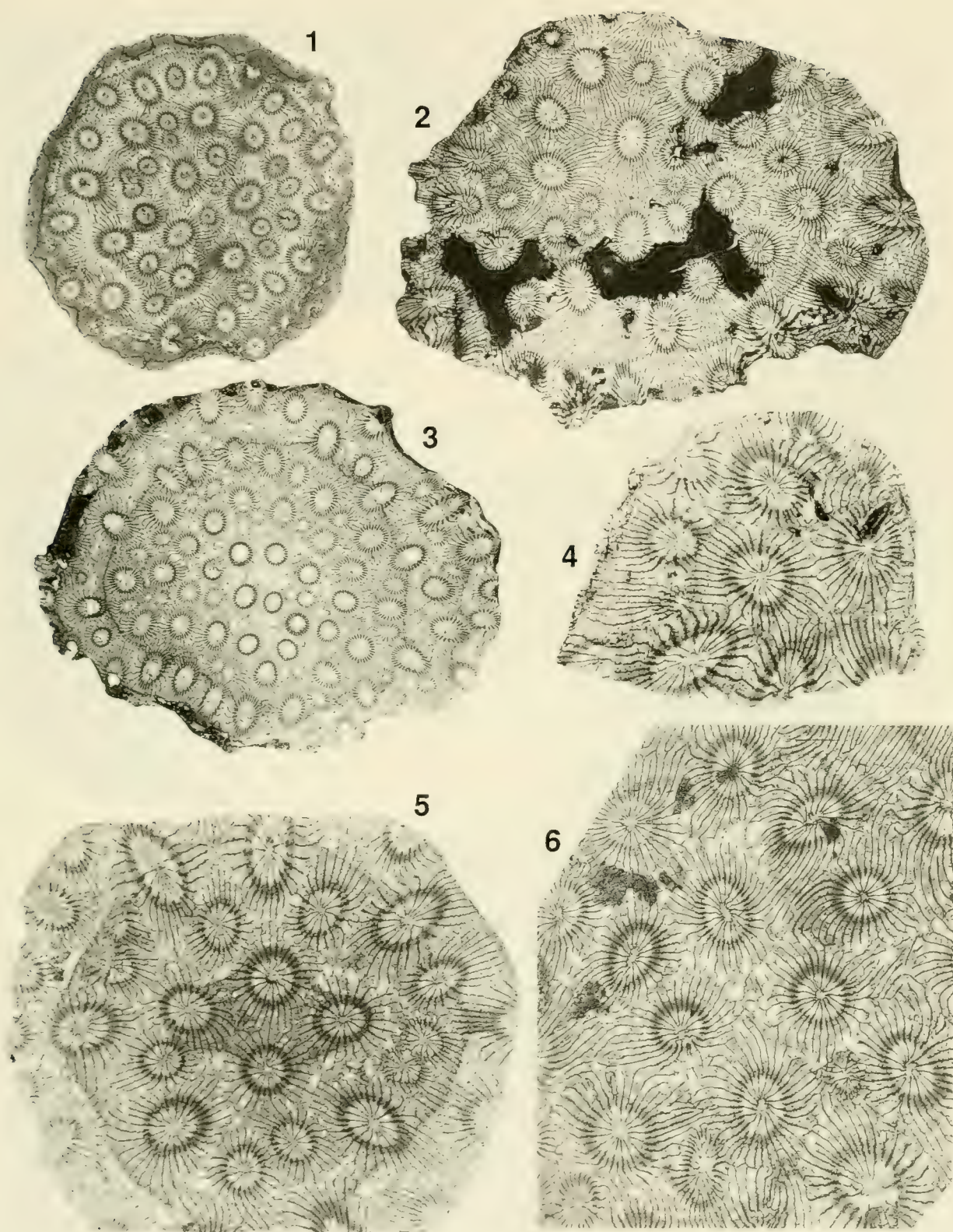


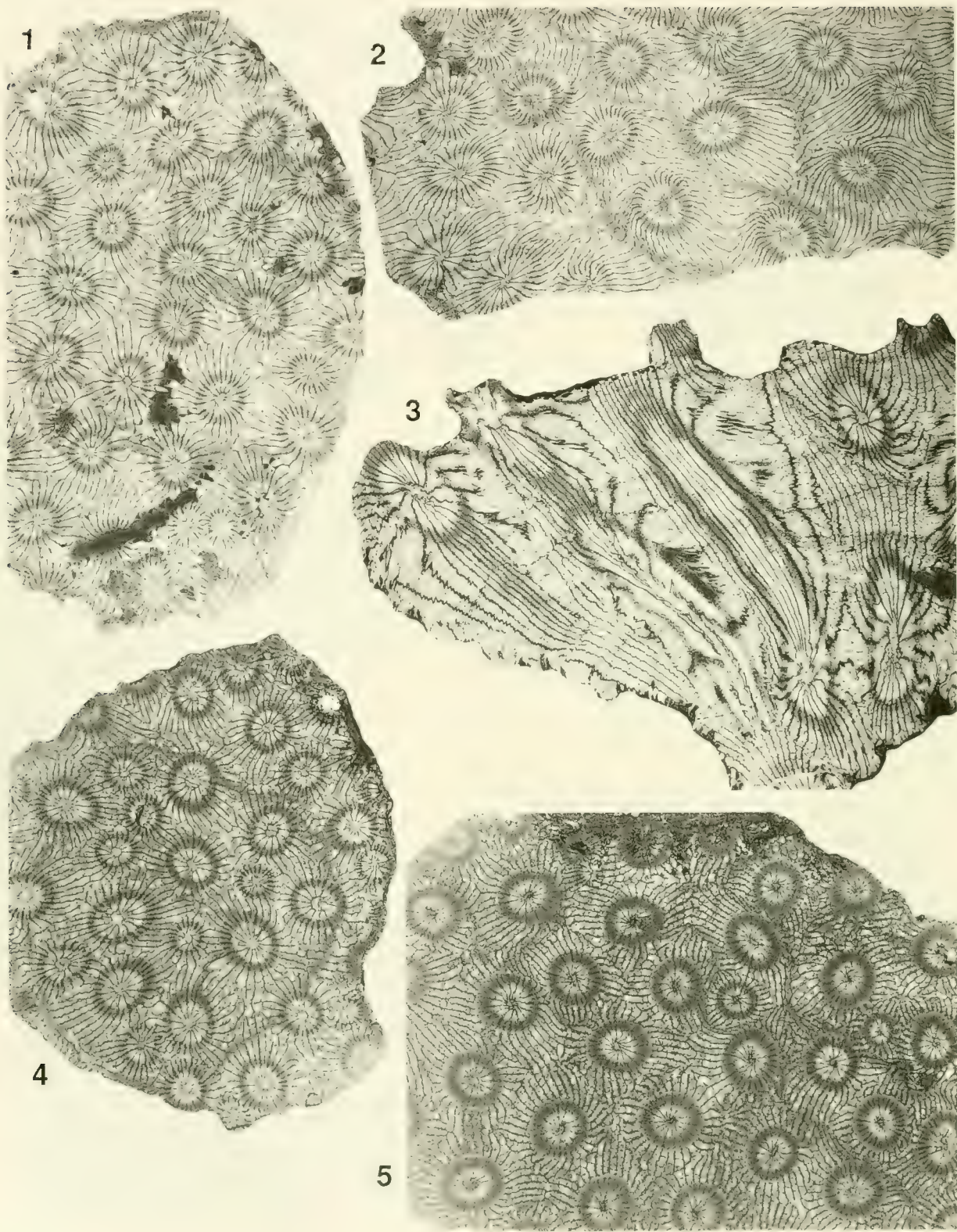
EXPLANATION OF PLATE 42

Figure	Page
1-6. <i>Pachyphyllum websteri</i> Belanski, 1928	76
1. P.R.I. 44791, transverse, of large, somewhat aphroid corallites with characteristic dilation of septa, $\times 2$.	
2. P.R.I. 44792, transverse of large corallites with budding, $\times 4$.	
3. S.U.I. 2176, holotype, longitudinal, illustrating irregular flat tabulae, uniform row horseshoe dissepiments with stereome on row, $\times 7$.	
4. P.R.I. 44793, transverse, illustrating stage of growth with large, irregular dissepiments, $\times 4$.	
5. P.R.I. 44794, transverse, showing adult budding to give off two offspring, $\times 4$.	
6. P.R.I. 44795, transverse, specimen apparently belonging to <i>P. websteri</i> , but occurring in Nora Member of Shell Rock Formation, $\times 2$.	

EXPLANATION OF PLATE 43

Figure	Page
1-6. <i>Pachyphyllum woodmani</i> Hall and Whitfield, 1873	78
1. P.R.I. 44802, transverse, colony with long septa, "aulos", and heavy septal dilation, $\times 1$.	
2. P.R.I. 44803, transverse, colony with short septa and open spaces at corallite axes, $\times 1$.	
3. P.R.I. 44804, transverse, colony with small diameter corallites, $\times 1$.	
4. N.Y.S.M. 3580/1, neotype, transverse, $\times 2$.	
5. P.R.I. 44805, transverse, colony strongly resembling neotype, $\times 2$.	
6. P.R.I. 44806, transverse, colony with variable development of dissepiments, $\times 2$.	



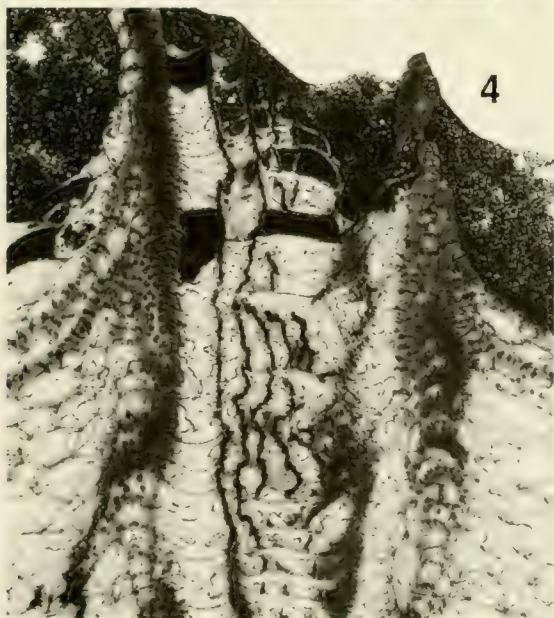
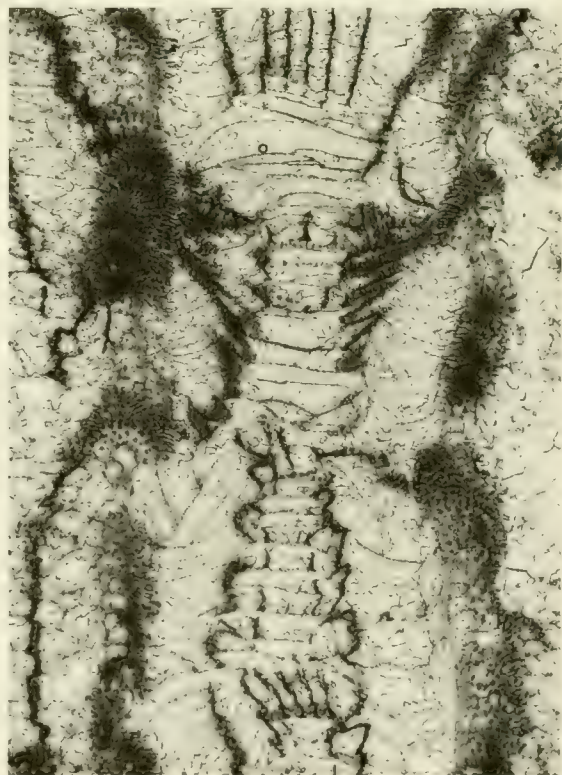
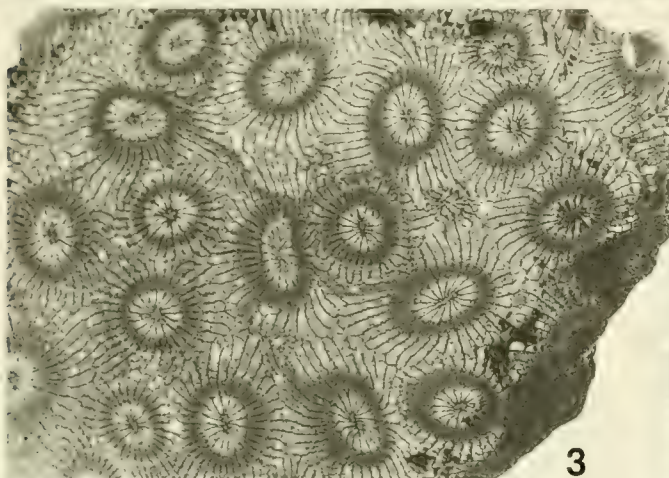
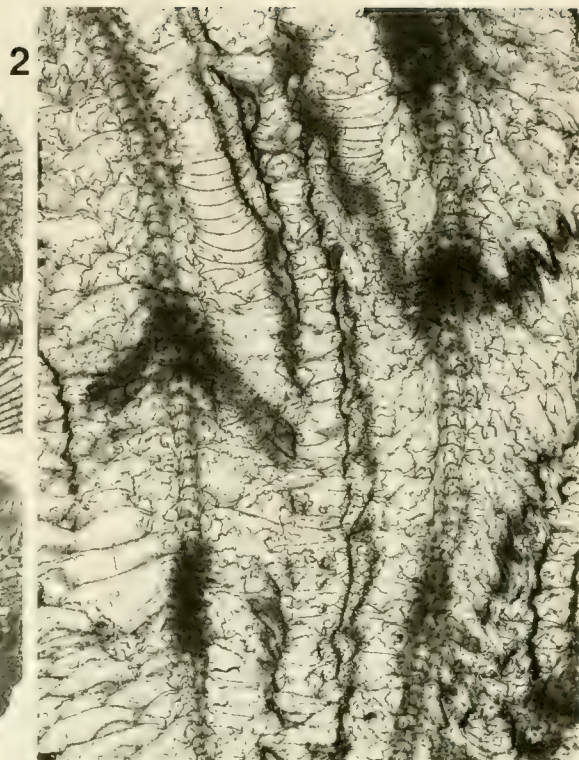


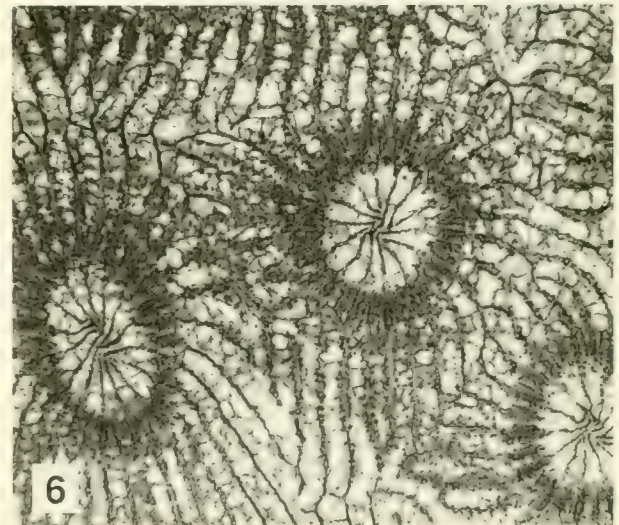
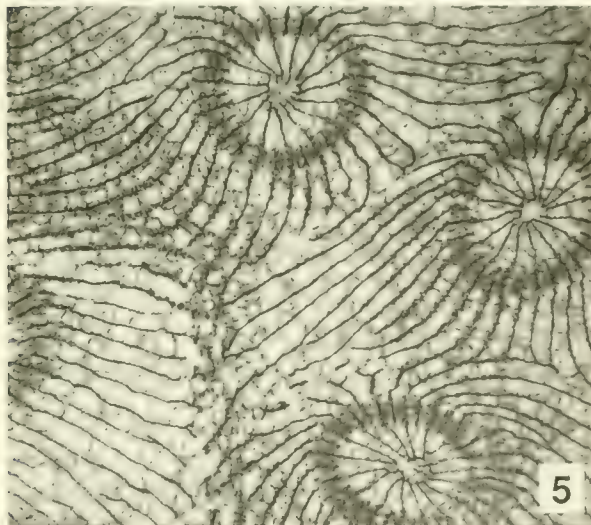
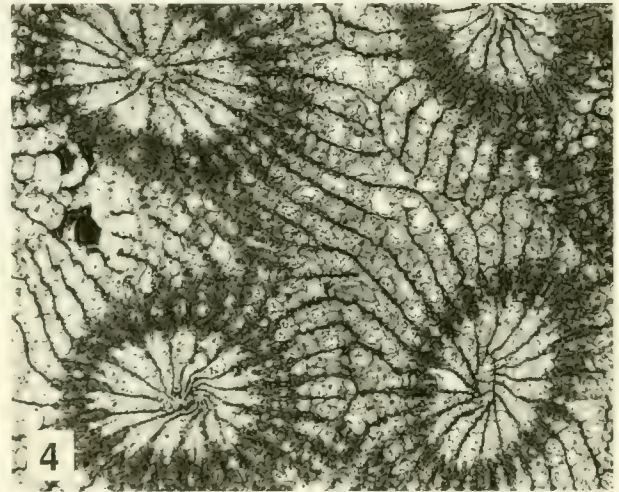
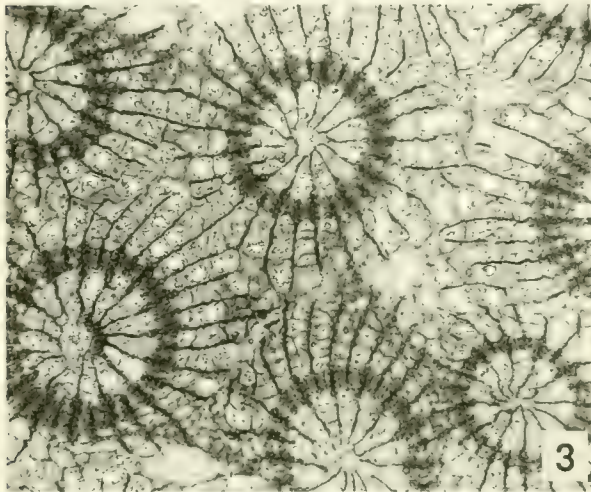
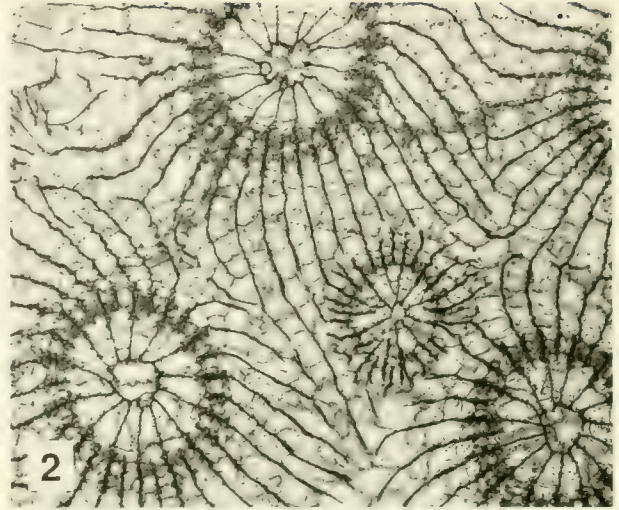
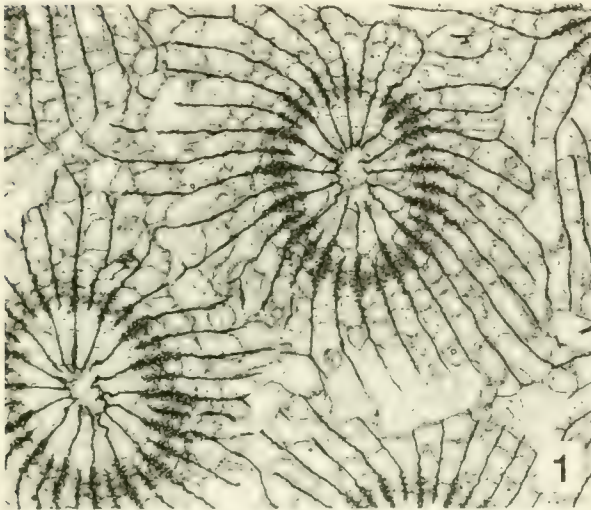
EXPLANATION OF PLATE 44

Figure	Page
1-5. <i>Pachyphyllum woodmani</i> Hall and Whitfield, 1873	78
1. P.R.I. 44807, transverse, colony with "typical" corallite size, $\times 2$.	
2, 3. U.S.N.M. 78629, holotype of <i>P. levatum</i> , a <i>P. woodmani</i> with moderately large corallites, 2. transverse, $\times 2$; 3. longitudinal, $\times 2$.	
4. P.R.I. 44808, transverse of colony with heavy septal dilation, $\times 2$	
5. P.R.I. 44809, transverse of colony with very heavy septal dilation over horseshoe dissepiments, $\times 2$.	

EXPLANATION OF PLATE 45

Figure	Page
1-5. <i>Pachyphyllum woodmani</i> Hall and Whitfield, 1873	78
1. U.S.N.M. 78646, holotype of <i>P. ordinatum</i> Webster, 1889, transverse, colony with heavy septal dilation and long septa, $\times 2$.	
2. U.S.N.M. 78629a, <i>P. levatum</i> holotype, longitudinal to illustrate uniform horseshoe dissepiments, $\times 9$.	
3. P.R.I. 44810, transverse, colony with long septa and very heavy septal dilation, $\times 2$.	
4. P.R.I. 44811, longitudinal, enlarged view of single corallite illustrating long septa, rhipidacanthine trabeculae and horseshoe dissepiments, $\times 9$.	
5. P.R.I. 44812, longitudinal, single corallite with rhipidacanthine septal trabeculae arranged in fans over horseshoe dissepiments, and tabularium with axial and periaxial rows of tabulae, $\times 9$.	



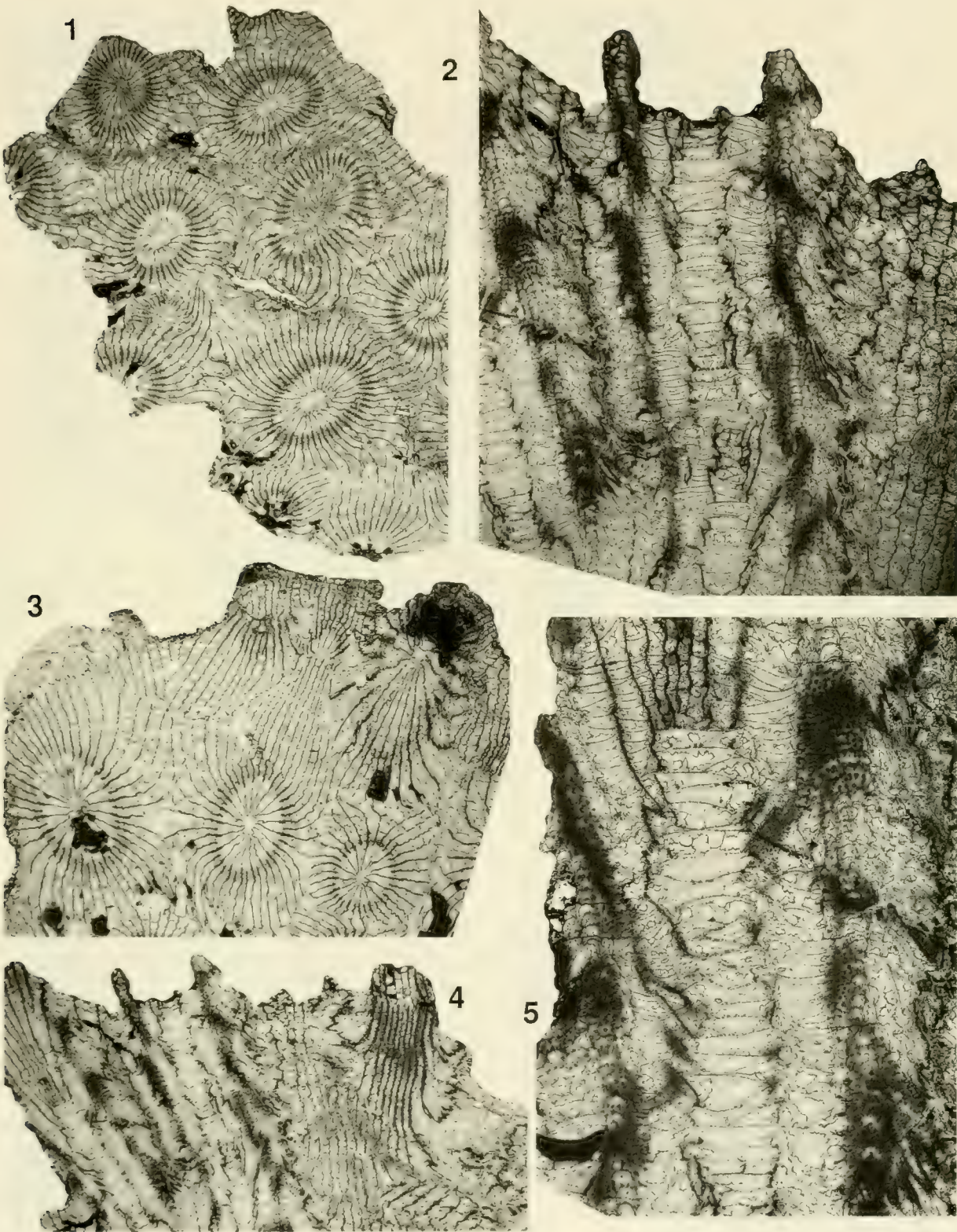


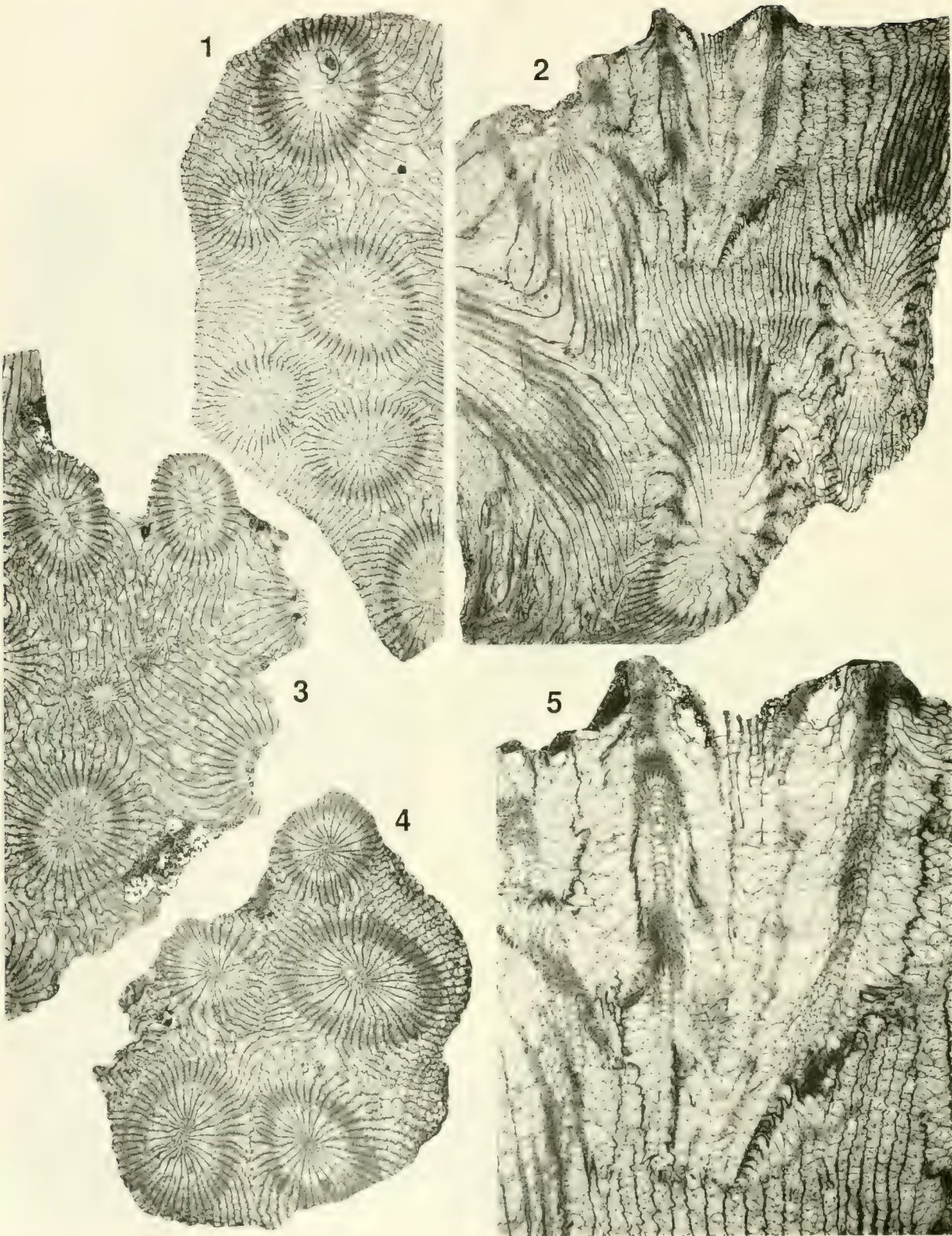
EXPLANATION OF PLATE 46

Figure	Page
1-6. <i>Pachyphyllum woodmani</i> Hall and Whitfield, 1873	78
1. P.R.I. 44813, transverse, corallites with light skeleton, aphroid in part, with moderate septal dilation and long septa, $\times 5$.	
2. P.R.I. 44814, transverse, corallites with confluent, complete septa, moderate dilation, and long septa with aulos, $\times 5$.	
3. P.R.I. 44815, transverse, corallites with heavy dilation over horseshoe dissepiments, $\times 5$.	
4. P.R.I. 44816, transverse, corallites with heavy dilation and long septa, $\times 5$.	
5. U.S.N.M. 78629, <i>P. levatum</i> holotype, transverse, with very heavy septal dilation forming solid ring around tabularium, and with long septa forming aulos at axis, $\times 5$.	
6. U.S.N.M. 78646, holotype of <i>P. ordinatum</i> , transverse, showing very heavy ring formed by dilated septa and heavy septa between corallites reflecting heavy, lumpy septal trabeculae, $\times 5$.	

EXPLANATION OF PLATE 47

Figure	Page
1-5. <i>Pachyphyllum woodmani</i> Webster and Fenton, 1924	78
1, 2. U.S.N.M. 78615, holotype of <i>P. irregulare</i> , 1. transverse, illustrating large corallites, $\times 2$; 2. longitudinal, enlarged to show steep-sided calicinal pit, $\times 4$.	
3. U.S.N.M. 78647, paratype of <i>P. irregulare</i> , transverse, $\times 2$.	
4, 5. U.S.N.M. 78615, holotype, 4. longitudinal, $\times 2$; 5. longitudinal, enlarged to illustrate rows of differentiated tabulae and horseshoe dissepiments, $\times 7$.	



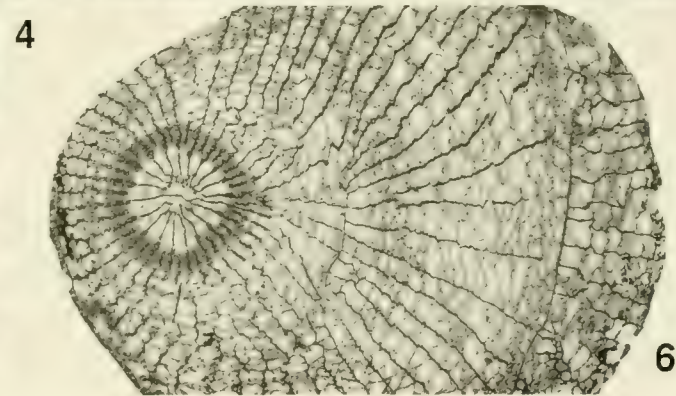
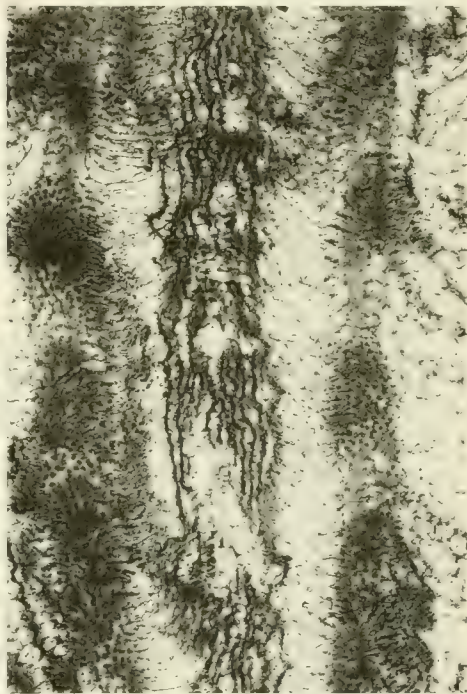
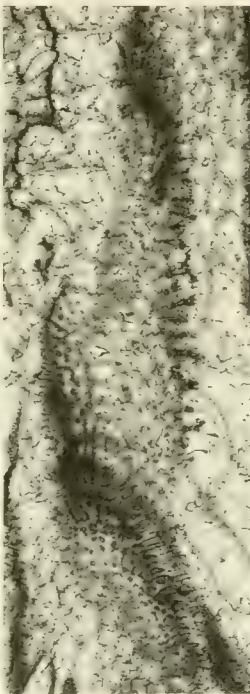
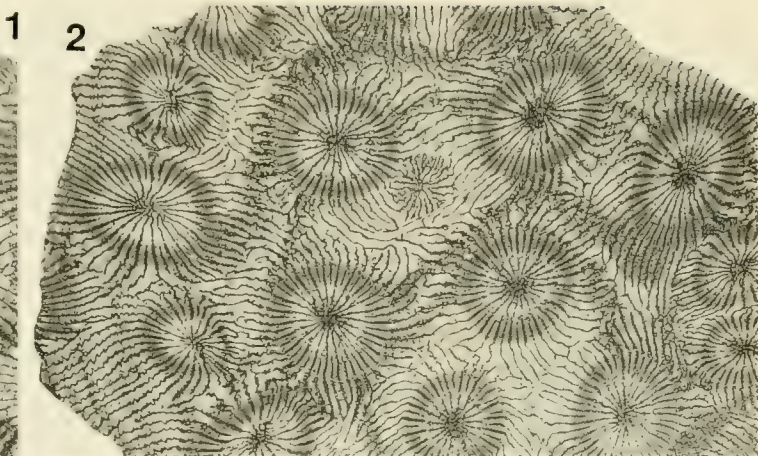
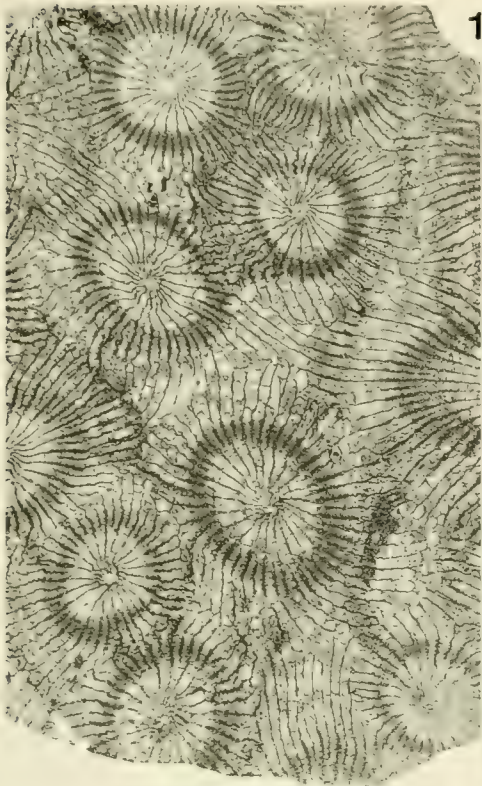


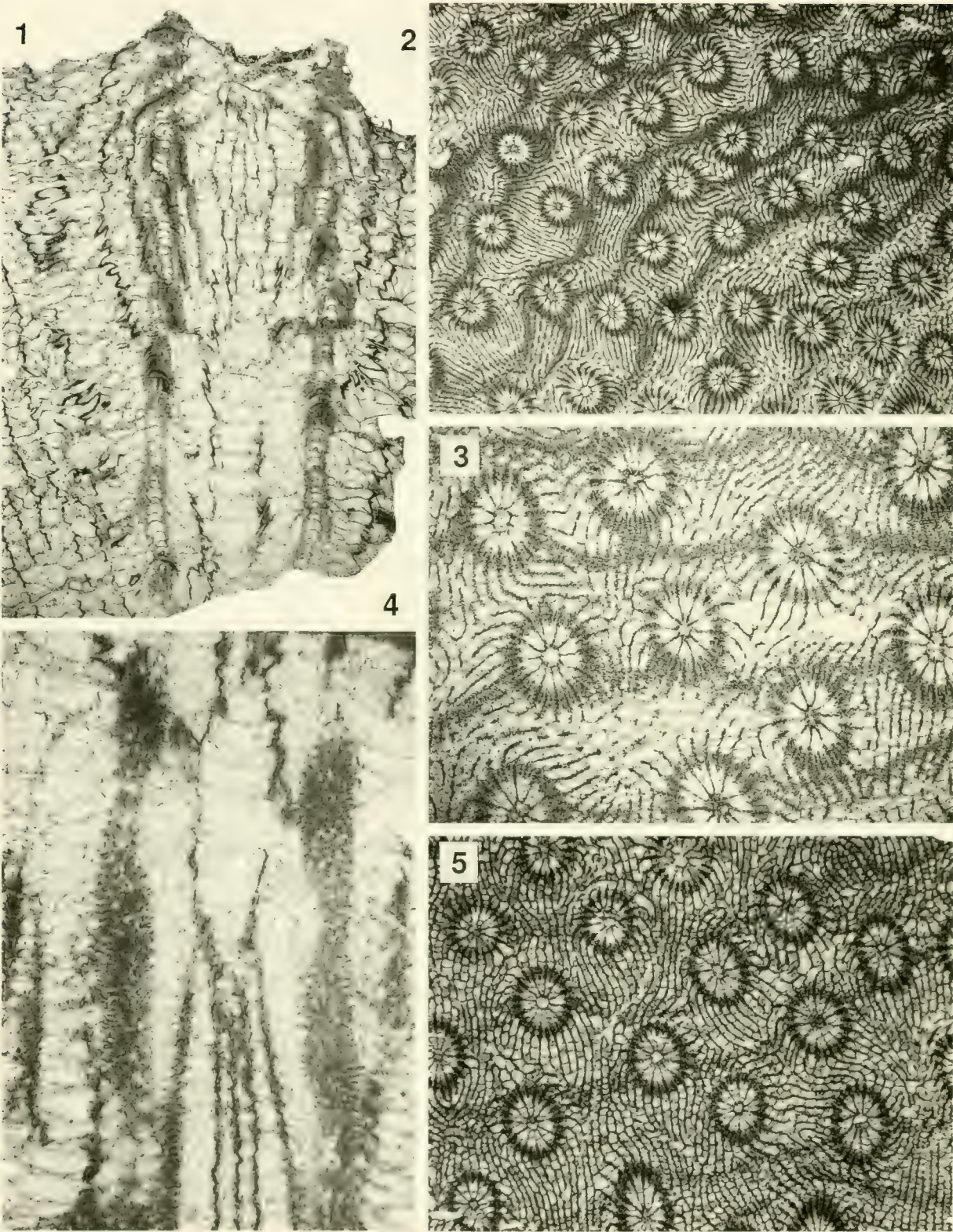
EXPLANATION OF PLATE 48

Figure	Page
1-5. <i>Pachyphyllum crassicostatum</i> Webster, 1889	80
1, 2. U.S.N.M. 78628A, lectotype, 1. transverse, with large corallites characterized by flat-sided septal dilation, $\times 2$; 2. longitudinal with corallites containing abundant irregular tabulae, $\times 2$.	
3. U.S.N.M. 78627, holotype of <i>P. owenense</i> , transverse, to show that this is just a small diameter colony of <i>P. crassiacostatum</i> , $\times 2$.	
4. U.S.N.M. 78628, lectoparatype, transverse of characteristic specimen, $\times 2$.	
5. U.S.N.M. 78628A, lectotype, longitudinal, to illustrate abundant incomplete tabulae and numerous dissepiments internal to the row of horseshoe dissepiments, $\times 4$.	

EXPLANATION OF PLATE 49

Figure	Page
1-6. <i>Pachyphyllum crassicostatum</i> Webster, 1889	80
1. P.R.I. 44817, transverse of specimen with typical septal dilation and with open area at axis, $\times 2$.	
2. P.R.I. 44830, transverse of specimen with small diameter confluent corallites, $\times 2$.	
3. U.S.N.M. 78628A, longitudinal of lectotype illustrating horseshoe dissepiments and fan-like configuration of coarse rhipidacanth trabeculae, $\times 9$.	
4. S.U.I. 3598, longitudinal of coarse, rhipidacanth septal trabeculae forming tooth-like extensions on margin of septum, $\times 9$.	
5. P.R.I. 44818, longitudinal of corallite with no internal dissepiments and very long septa making an irregular axial structure, $\times 7$.	
6. P.R.I. 44819, transverse of founder corallite of a colony, $\times 4$.	



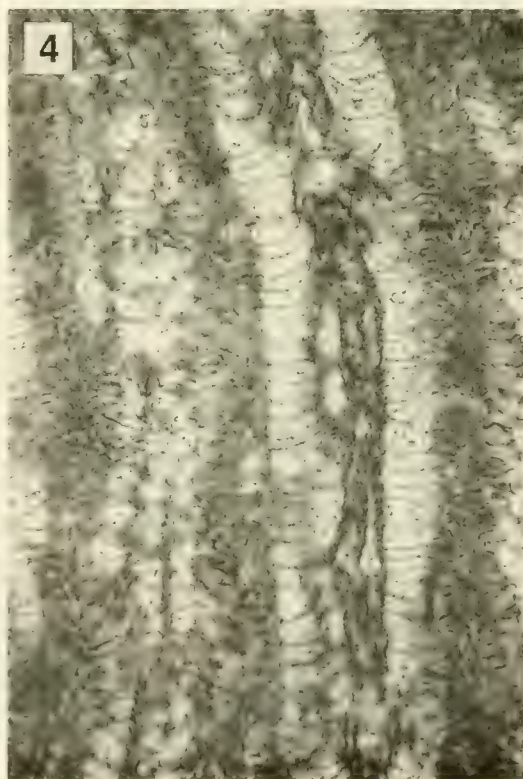
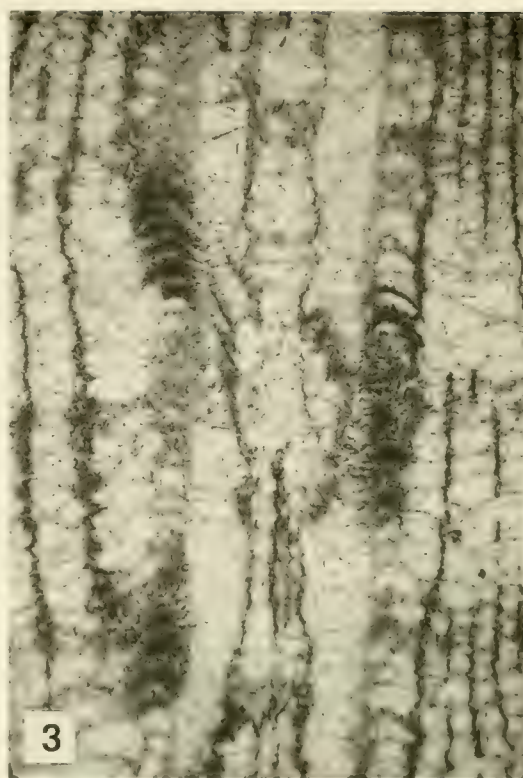
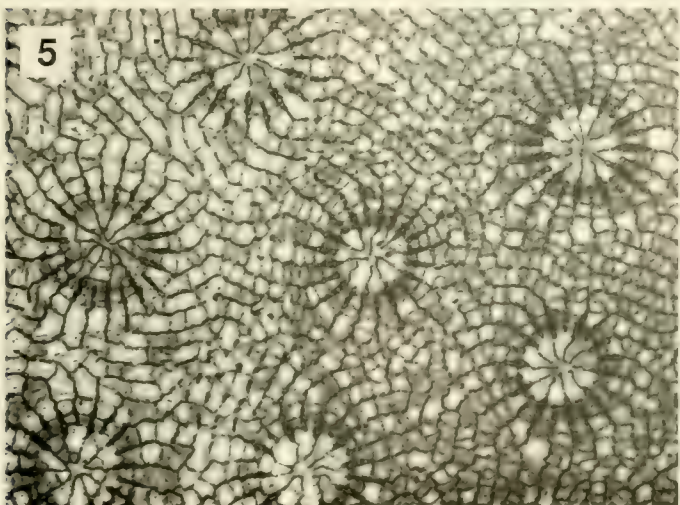
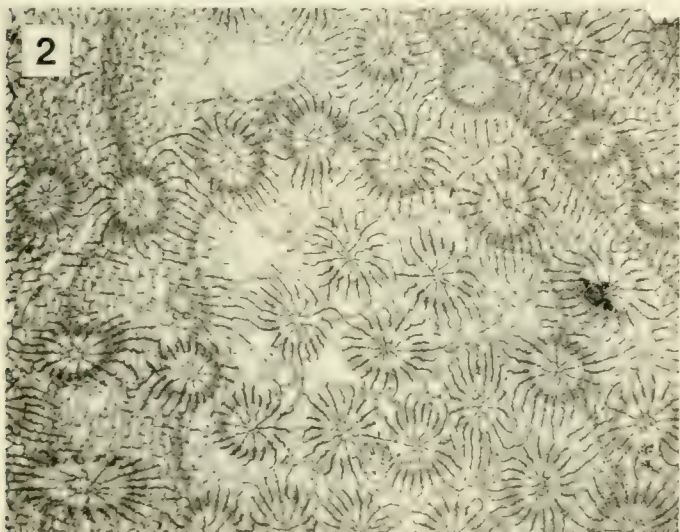
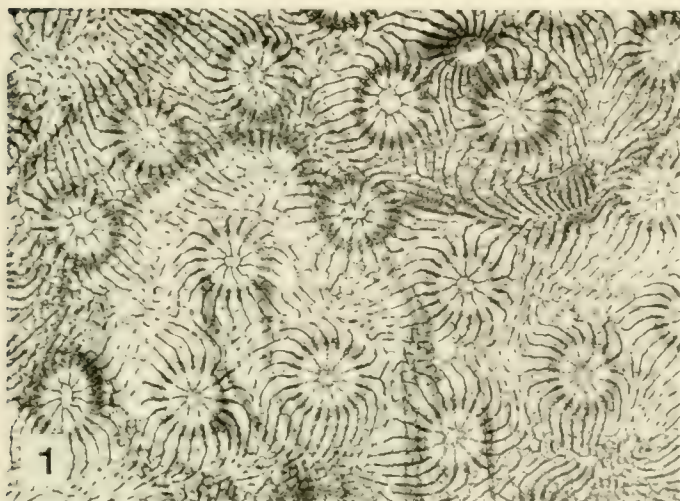


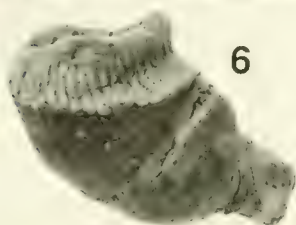
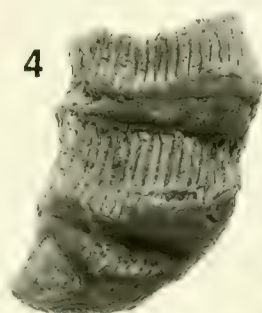
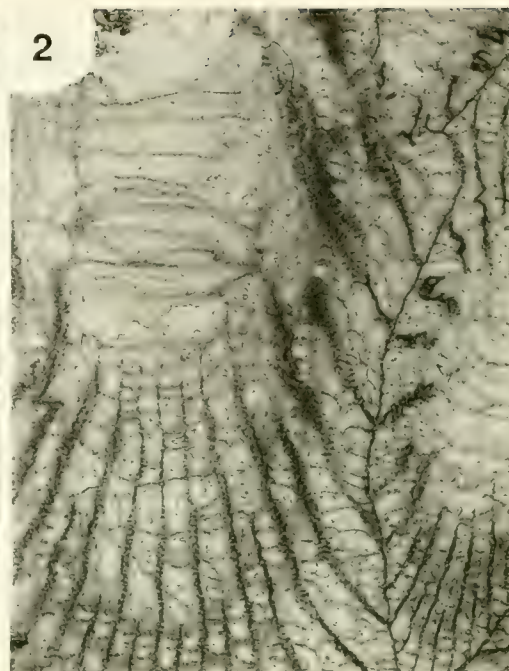
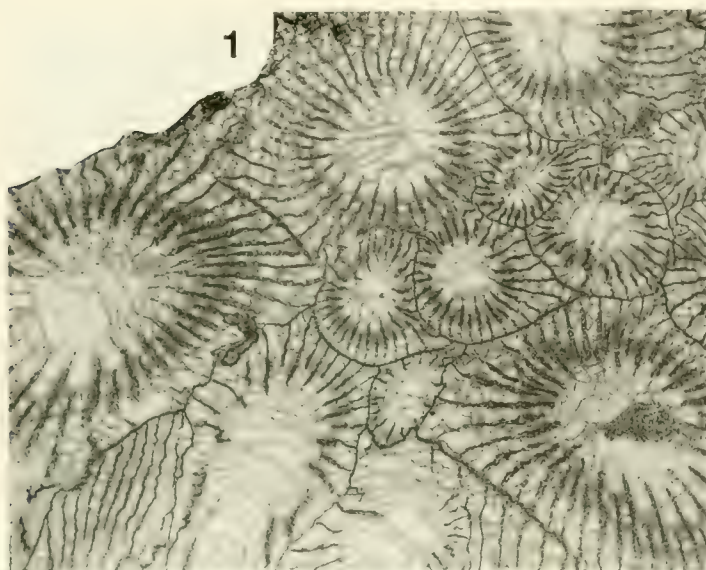
EXPLANATION OF PLATE 50

Figure	Page
1. <i>Pachyphyllum crassicostatum</i> Webster, 1889	80
1. U.S.N.M. 78627, paratype of <i>P. owenense</i> , longitudinal, showing stereome deposited on row of horseshoe dissepiments, $\times 4$.	
2-5. <i>Pachyphyllum dumonti</i> n. sp.	82
2, 3, 4. P.R.I. 44820, holotype, 1. transverse, $\times 2.5$; 3. transverse, enlarged to show long septa and aulos, $\times 6$; 4. longitudinal enlarged to show septal trabeculae and incomplete tabulae, $\times 15$.	
5. P.R.I. 44821, paratype, transverse, with very small corallites and clearly formed aulos, $\times 5$.	

EXPLANATION OF PLATE 51

Figure	Page
1-5. <i>Pachyphyllum dumonti</i> n. sp.	82
1. P.R.I. 44822, paratype, transverse, to show various weight of skeleton at different growth stages of colony, $\times 5$.	
2. P.R.I. 44823, transverse of colony that was aphroid at some stages of its growth history, $\times 5$.	
3, 4. P.R.I. 44822, longitudinal; 3. illustrating horseshoe dissepiments that are irregularly developed, $\times 10$; 4. corallite with regular periaxial tabulae interrupted by long septa at axis, $\times 10$.	
5. U.S.N.M. 98282, holotype of <i>P. nevadense</i> , transverse, with development of dissepiments of near uniform size as show by intersections, $\times 5$.	



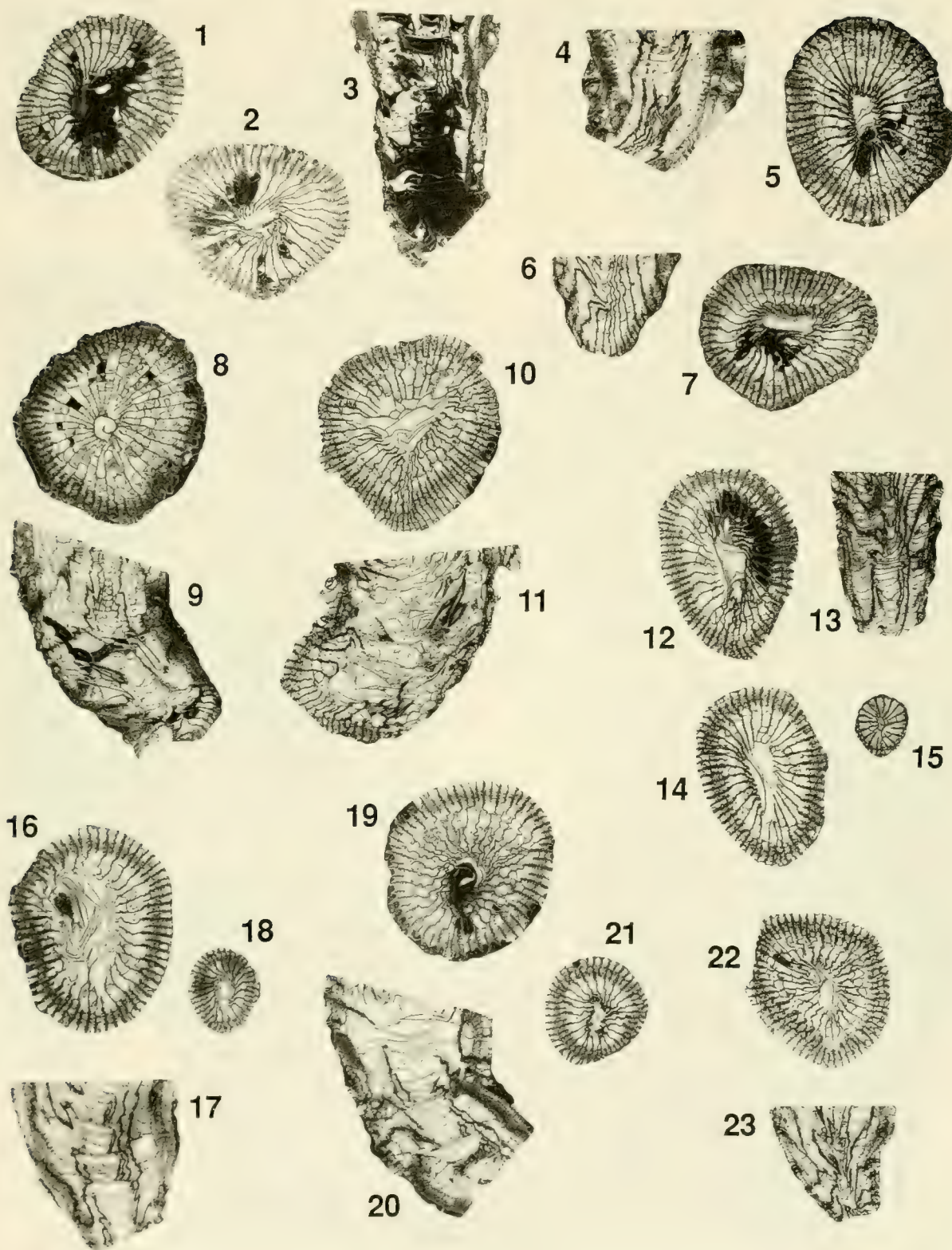


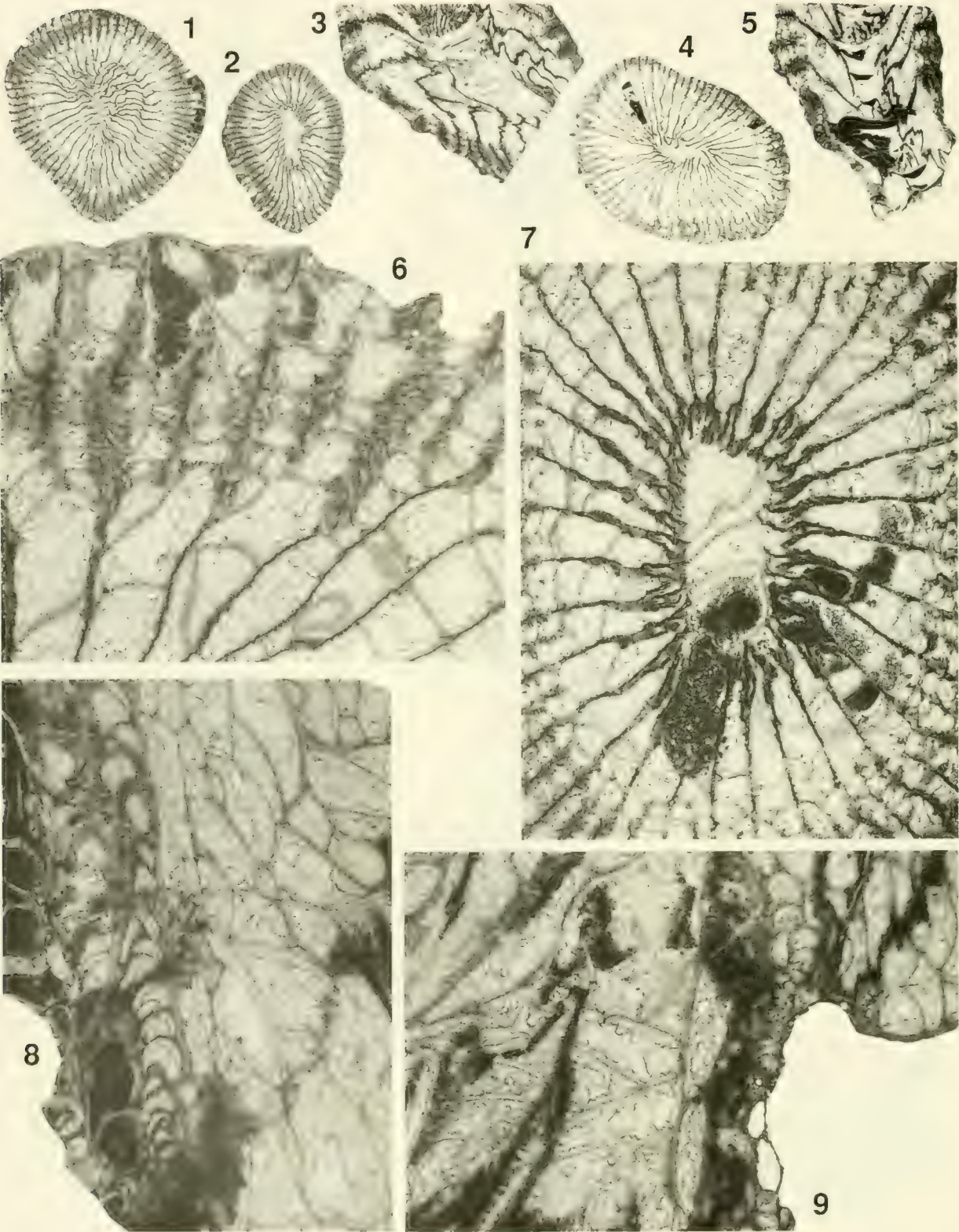
EXPLANATION OF PLATE 52

Figure	Page
1-3. <i>Trapezophyllum</i> sp. A	84
1, 2, 3. P.R.I. 44824, 1. transverse in colony with transverse and longitudinal cross sections of mature and juvenile corallites, $\times$ 4; 2. longitudinal to show variable development of outer dissepiments, including ladder-like forms (arrow), $\times$ 6; 3. longitudinal with horseshoe dissepiments, $\times$ 7.	
4-8. <i>Macgeea solitaria</i> (Hall and Whitfield, 1873)	86
4. U.S.N.M. 135374, $\times$ 2.	
5. U.S.N.M. 135381, $\times$ 2.	
6. U.S.N.M. 78449c, $\times$ 1.9	
7. U.S.N.M. 48449a, neotype of species, external, $\times$ 2.	
8. U.S.N.M. 32706b, $\times$ 1.9.	

EXPLANATION OF PLATE 53

Figure	Page
1-23. <i>Macgeea solitaria</i> (Hall and Whitfield, 1873)	86
Series to illustrate variation in topotype population.	
1, 2, 3. U.S.N.M. 48449a, neotype, 1. transverse at calice, $\times 2$; 2. transverse lower in corallite, $\times 2$; 3. longitudinal, $\times 2$.	
4, 5. U.S.N.M. 135374, 4. longitudinal, $\times 2$; transverse, $\times 2$.	
6, 7. U.S.N.M. 135381, 6. longitudinal, $\times 2$; transverse, $\times 2$.	
8, 9. U.S.N.M. 2273b, 8. transverse, $\times 2$; longitudinal, $\times 2$.	
10, 11. U.S.N.M. 78449d, 10. transverse, $\times 2$; longitudinal, $\times 2$.	
12, 13, 14, 15. U.S.N.M. 78449f, 12. transverse at calice, $\times 2$; 13. transverse, $\times 2$; 14. longitudinal, $\times 2$; 15. juvenile, $\times 2$.	
16, 17, 18. U.S.N.M. 32706a, 16. transverse, $\times 2$; 17. longitudinal, $\times 2$; juvenile, $\times 2$.	
19, 20, 21. U.S.N.M. 32706b, 19. transverse, $\times 2$; 20. longitudinal, $\times 2$; juvenile, $\times 2$.	
22, 23. U.S.N.M. 32706d, 22. transverse, $\times 2$; 23. longitudinal, $\times 2$.	



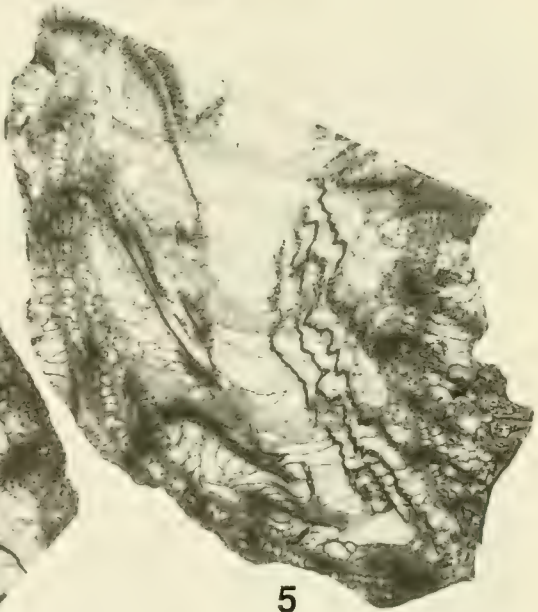
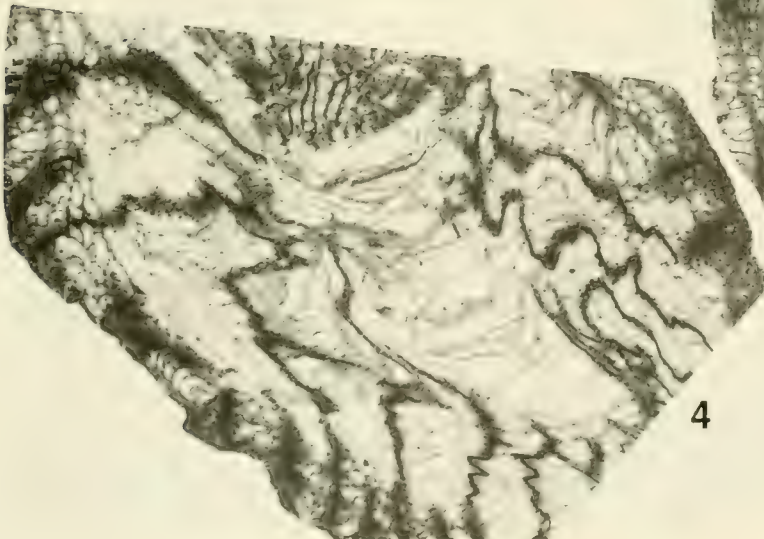
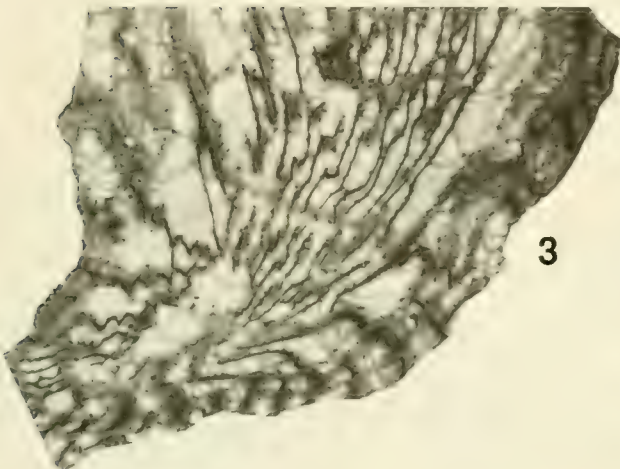
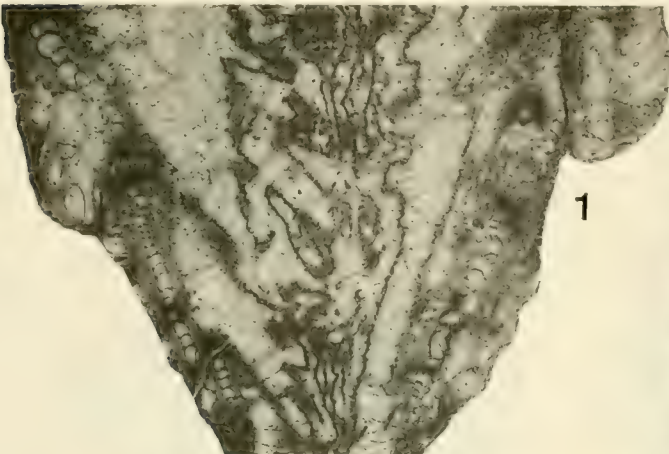


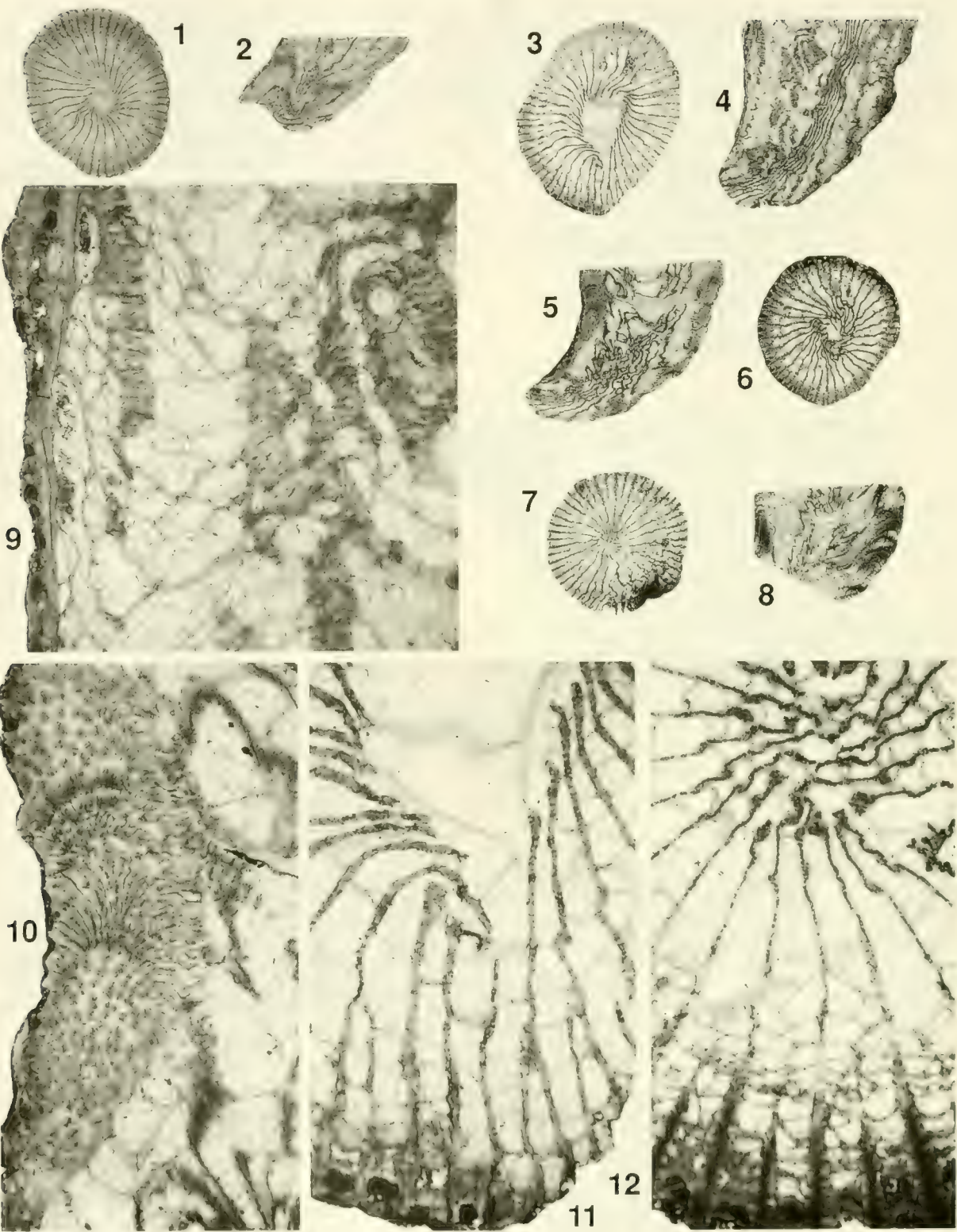
EXPLANATION OF PLATE 54

Figure	Page
1-9. <i>Macgeea solitaria</i> (Hall and Whitfield, 1873)	86
1, 2, 3. U.S.N.M. 53181, 1. transverse, $\times 2$; 2. transverse in youthful part of corallite, $\times 2$; 3. longitudinal, $\times 2$.	
4, 5. P.R.I. 44825, 4. transverse, $\times 2$; 5. longitudinal, $\times 2$.	
6. U.S.N.M. 78449a, neotype, transverse, illustrating typical septal dilation, $\times 14$.	
7. U.S.N.M. 135374, transverse, axial part of septa almost forming aulos, $\times 8$.	
8. U.S.N.M. 2273b, longitudinal, showing horseshoe row of dissepiments and irregular single row of external dissepiments, $\times 12$. Outermost are encrusting aulopodid corals (arrow).	
9. U.S.N.M. 78449d, longitudinal, enlarged to show lateral expansion of outer dissepimentarium and numerous dissepiments developed as corallite expanded over soft substrate, $\times 12$.	

EXPLANATION OF PLATE 55

Figure	Page
1-5. <i>Macgeea solitaria</i> (Hall and Whitfield, 1873)	86
Series to illustrate variation in longitudinal section.	
1, 2. U.S.N.M. 2273a, 1. multiplicity of external dissepiments in more adult part of corallite, $\times 7$; 2. enlargement to illustrate lateral expansion on soft substrate, $\times 12$.	
3. U.S.N.M. 20722A, corallite with long septa, interrupted tabulae, and few irregular external dissepiments, $\times 5$.	
4. U.S.N.M. 53181, individual with several rows of internal dissepiments, sparse and irregular external dissepiments, $\times 5$.	
5. U.S.N.M. 7798A, corallite with sparse, flattish external dissepiments and heavy stereome coating on horseshoe dissepiments as well as heavy, stereome-coated tabulae at several levels, $\times 5$.	



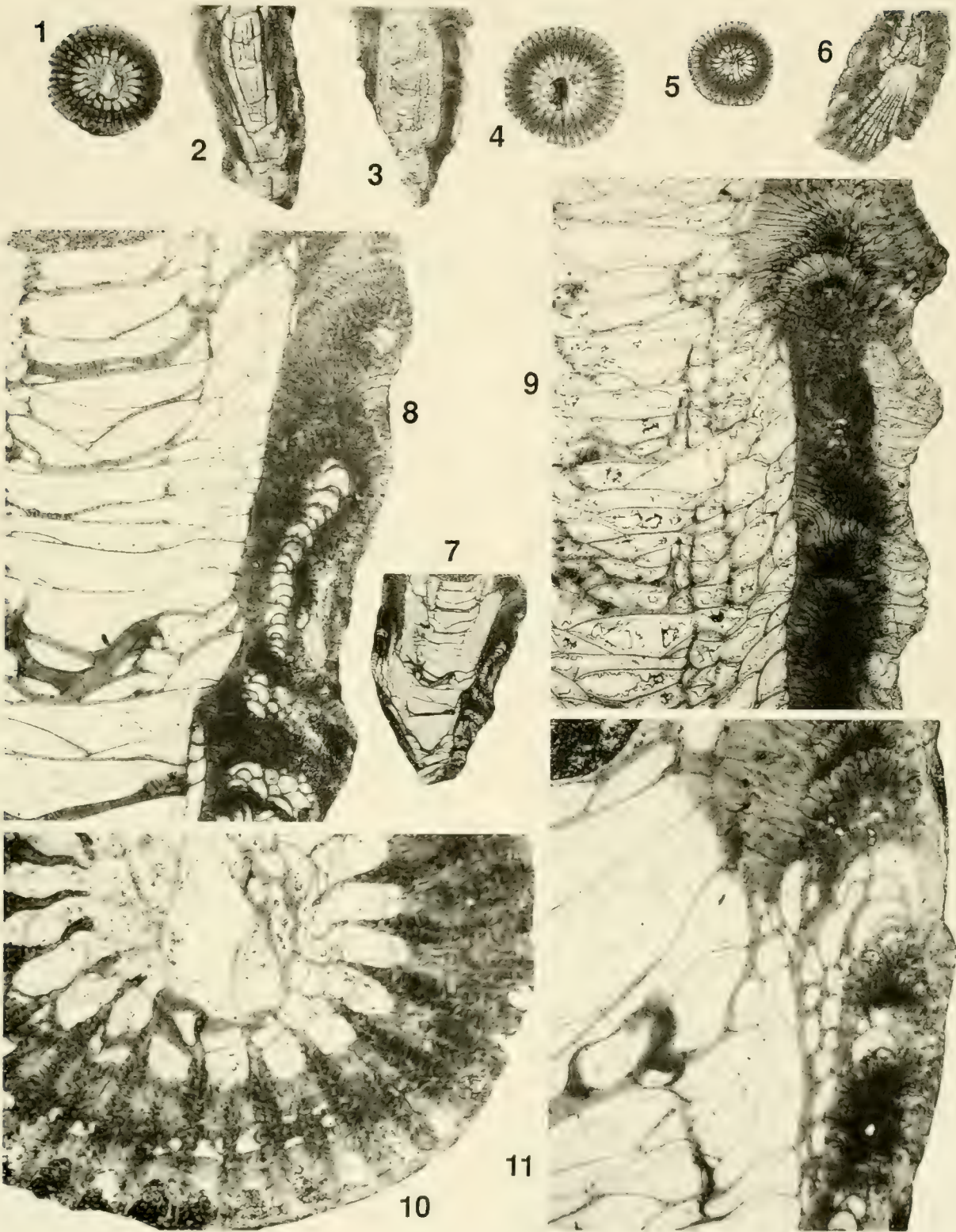


EXPLANATION OF PLATE 56

Figure	Page
1-12. <i>Macgeea camplanulata</i> n. sp.	89
1. 2. S.U.I. 3490, holotype, 1. transverse, $\times 2$; 2. longitudinal, $\times 2$.	
3. 4. P.R.I. 44826, paratype, 3. transverse, $\times 2$; 4. longitudinal, $\times 2$.	
5. 6. P.R.I. 44827, paratype, 5. longitudinal, $\times 2$; 6. transverse, $\times 2$.	
7. 8. P.R.I. 44828, paratype, 7. transverse of long-septaed corallite, $\times 2$; 8. longitudinal, $\times 2$.	
9. P.R.I. 44826, paratype, longitudinal, enlarged, with heavy stereome coating on horseshoe dissepiments and numerous internal dissepiments, $\times 10$.	
10. P.R.I. 44827, paratype, enlargement of septal structure typified by fans of rhipidacanthine septal trabeculae, $\times 12$.	
11. P.R.I. 44826, paratype, transverse of coral with short septa and shorter cardinal septum, $\times 10$.	
12. P.R.I. 44829, transverse of long-septaed corallite with irregular ends of septa forming a loose axial structure, $\times 10$.	

EXPLANATION OF PLATE 57

Figure	Page
1-11. <i>Macgeea concinnula</i> n. sp.	90
1, 2. S.U.I. 1257, holotype, 1. transverse, $\times 2$; 2. longitudinal, $\times 2$.	
3, 4. S.U.I. 1252, paratype, 3. longitudinal, $\times 2$; 4. transverse, $\times 2$.	
5, 6. S.U.I. 1256, paratype, 5. transverse, $\times 2$; 6. longitudinal, $\times 2$.	
7, 8. S.U.I. 1258, paratype, 7. longitudinal, $\times 2$; 8. enlarged to illustrate tight fans of septal trabeculae and variable development of "normal" external dissepiments, $\times 8$.	
9. S.U.I. 1252, paratype, longitudinal of coral with heavy, tight fan of septal trabeculae over horseshoe dissepiments, numerous internal dissepiments, and sparse, flattish external dissepiments, $\times 9$.	
10. S.U.I. 1257, holotype, transverse, enlarged to show heavy coat of stereome on horseshoe dissepiments to form a solid ring around the tabularium, $\times 10$.	
11. S.U.I. 1258a, paratype, enlarged longitudinal, with clustering of several rows of internal dissepiments with horseshoe dissepiments under tight fan of septal trabeculae, $\times 12$.	



INDEX

Note: Page numbers for descriptions of genera and species are shown in **bold type**.

- Acervularia* 68
 "Acervularia zone" 20,22
Actinostroma, "Actinostroma zone" 12,17
Alveolites 16
 amplexoid septa 33,36,39,40,42,43,44,47,49,55,56,115,119
 aphroid, 28,30,31,75,76,77,78,82,138,141,145,150
Apolythophyllum 34
Argutastrea 64
 aulos 78,83,142,145,149,153
 axial boss 34,39,42,43
 axial and peri-axial tabulae ... 28,31,63,64,66,68,129,130,133,144
- Belanski, C.H. 8,12,27
 bilateral symmetry 34,41,42,44
Bullingsastrea 71
 biostratigraphy 21
 Cyrtospirifer whitneyi Zone 22,23
 Douvillina arcuata Zone 23
 Elita inconsueta Zone 23
 Iowatrypa owenensis Zone 22,23
 Lingula fragila Zone 22
 Nervostrophia thomasi Zone 23
 Strophodonta cicatricosa Zone 21,22
 Tenticospirifer shellrockensis Zone 21,22
 Bird Hill 17,23,26
- "carinate" septa 54,57,59,60,64,66,67,131,133
 Cedar Valley Group 9,22
 Lithograph City Formation 9,22
 Characterophyllidae 53,57
Characterophyllum 8,53,57
 C. nanum 53,54-57,101,123,124,125
 amplexoid septa in 55
 "carinae" in 54
 septal trabeculae in 54,55,124
Chonophyllum 33,37
Chuanbeiphyllum 72
Columnaria 58
 confluent septa 75,76,78,81,83,137,145
Cyathophyllum 57,63
 C. marginatum 86
Cyrtospirifer 19
Cystihexagonaria 64
- Debnikiella* 86
 denticulate septa 55,56,59
Diphyphyllum 58,59
 Disphyllidae 53,57
Disphyllum 8,57,58
 D. caespitosum 59,61,63
 D. conjugans 61-62,100,127,128
 D. dispassum 58-59,125
 D. fasciculum, 58,59,61,62,63
 D. floxense 59-61,100,126,127
 D. rowensis 62-63,100,128
 D. kostetskae 63
 D. rugosum 63
 D. tubiforme 59
 peripheral dissepiments in 58,59,60,61,62,127,128
- septal dilation in 58,60,61
 septal trabeculae in 58,60,62,63,126
Diversophyllum 34
Douvillina 17
 Dumont, Iowa 19
- edge zone 85,87
 Endophyllidae 27,51
 exsert corallites 78,80
- Famennian 23,34
 Fenton, C., and Fenton, M. 8,15,19,25,29,33,38
Floydia beds 17,19,20
 Frasnian 7,8,22
Frechastraea 72,73
 "fucoid beds, rusty bed" 16,17
- Gracilirectus* 17
 Greene, Iowa 15
 growth (seasonal?) banding 29,34,60,77,83,105,138
- Hackberry Stage 8,14
 Hall, J., and Whitfield, R.P. 8,25,28,38
Haplothechia 57
Heliophyllum 54,56,59,64,65
Hexagonaria 16,63-64
 "carination" of septa 65,67,69,131,133
Acervularia whitfieldi 69
 H. bassleri 19,21,64,64-67,68,101,129,130,131
 H. bassleri bassleri 66
 H. bassleri depressa 66
 H. bassleri magna 66,67,131,132
 H. buxutiensis 66
 H. hexagona 57,64,65,67,68,69
 H. inequalis 68-70,101,133,134,135
 H. oweni 64,67-68,100,132,133
 H. mae 66
 H. marmini 66
 H. reticulata 66
 septal dilation in 63,64,65,69,132,133,135
 septal trabeculae in 63,64,65,68,69,130,135
 tabulae, axial and periaxial rows of 63,64,65,68
- Hill, D. 24,25,27,34,57,64,70
 horseshoe dissepiments .. 70,71,72,74,75,77,81,83,85,87,88,89,
 90,91,136,137,138,139,140,141,143,144,146,149,153,155,156
Idiostroma beds (*Amphipora*) 17,18
Iowaphyllum 8,16,27,28-31,70
 I. johanni 24,28,30, 31-33,101,103,104,105
 I. marginatum 24,30,31,32
 I. multiradiatum 24,30,31,32
 I. nisbeti 30,32
 aphroid coralla in 28,30,31
 axial and peri-axial tabulae in 28,31
 intercorallite "walls" in 28,30,31,32
 septal crusts and ridges in 28,29,30,31,32,103,104,105
- Kyphophyllidae 33,49,51

- Leptostrophia canace* 17
- Lime Creek Formation 7,8,14,21,22,24
- Cerro Gordo Member 14,15,21,24
- Juniper Hill Member 14,22,23,24
- Owen Member 17,18,20,23,24
- lonsdaleoid dissepimentarium 33,35,36,37,44,46,118
- Macgeea* 8,72,85-86
- M. bathycalyx* 88
- M. camplanulata* 88,89-90,155
- M. carnockii* 91
- M. concinnula* 90-91,156
- M. dubia* 88
- M. gallica* 86,88,90
- M. multizonata* 88,90
- M. solitaria* 86-89,90,151,152,153,154
- M. (Macgeea)* 86
- M. (Thamnophyllum)* 86
- edge zone in 85,87
- horseshoe dissepiments in 85,87,88,89,90,91,153,155,156
- nomen oblitum* 86
- Pterorrhiza* 85,86
- rhipidacanth septal trabeculae in 85,87,88,91,156
- septal dilation in 87,89,90,153
- trabecular fans in 85,87,91,156
- tripartite dissepimentarium in 87,88,89,90,154
- Marble Rock, Iowa 9,10,14,16
- Marisastrum* 57
- Mason City, Iowa 15
- Medusaeophyllum* 70,71,72
- monacanth trabeculae, coarse 54,55,58,60,62,63,64,65,68,
..... 69,126,130,135
- monacanth trabeculae, fine 34,40,41,43,45,47,48,108,
..... 111,114,117,118
- Montagne Noire conodont zones 22, 23
- Mourlonia* beds 17
- Nervostrophia* 16
- Nora Springs, Iowa 11,12,13,14,18,19
- Owen Grove, Iowa 15,16,22,26
- Pachyphyllum* 8,16,19,70-73
- P. anfractum* 82
- P. bouchardi* 70,71
- P. chenouensis* 71
- P. confluent* 75
- P. crassicosatum* 21,72,73,80-82,90,101,147,148,149
- P. crassicosatum nanum* 79
- P. disrupta* 76
- P. dumonti* 82
- P. exigua* 74
- P. gregarium* 75-76,138,139
- P. ibergense* 77
- P. irregulare* 79
- P. levatum* 79
- P. minutissimum* 73-75,136,137
- P. mirusensis* 81
- P. nevadensis* 74
- P. ordinatum* 79
- P. owenense* 81,82
- P. variabile* 75
- P. websteri* 76-78,140,141
- P. woodmani* 72,73,78-80,101,102,142,143,144,145,146
- P. woodmani avocaensis* 82
- aphroid septa in 75,76,77,78,82,138,141,145,150
- "aulos" in 78,83,142,145,149
- exert corallites in 78,80
- founder corallite in 78,80
- growth banding in 82,138
- horseshoe dissepiments in 70,71,72,74,75,77,81,83,136,137,
..... 138,139,140, 141,143,144,146,147,149
- rhipidacanth trabeculae in 72,74,80,81,83,144,148
- septal confluency in 75,76,78,81,83,137,145
- septal dilation in 70,73,75,76,77,78,79,81,83,136,137,
..... 139,143,144,145
- septal trabeculae in 70,74,75,77,81,137
- trabecular fans in 71,74,137
- Parasmithiphyllum* 51
- Peneckiella* 58,62
- peripheral sag of tabulae 33,35,36,37,38,39,40,42,43,110,112
- Pexiphyllum* 86
- Phillipsastrea* 70,71,72,73
- P. hennahi* 73
- Phillipsastreidae 57,64,70
- Portland, Iowa 16
- presepiments 33,34,35,36,37,38,40,41,42,44,46,47,105,
..... 106,119,121,122
- Pseudohexagonaria* 64
- Pterorrhiza* 85,86
- rhipidacanth trabeculae 72,74,80,81,85,87,88,91,144,148
- Rockford, Iowa 9,11,13,14,15,17,20,26,
- Rockwell, Iowa 19,21,23,26,27
- Roseville, Iowa 15
- Rozkowskaella* 86
- Rudd, Iowa 20
- septal crusts and ridges 28,29,30,31,32,103,104,105
- septal trabeculae 49,52,56,57,58,60,62,63,70,74,75,77,81,
..... 111,117,114,126,130
- septal dilation 38,40,42,46,58,60,61,63,70,73,75,76,77,
..... 78,79,81,83,132,135,136,139,144,145,153
- septotheca 34,37,40,41,45,48,49,50,52,115,118
- Shell Rock Formation 7,8,9,21,22
- Mason City Member 9,16,21,22
- Nora Member 11,12,21,22
- Rock Grove Member 10,11
- Shell Rock River 9,12,13,16,18,19
- Sinospongophyllum* 34
- Smithia* 32
- S. multiradiata* 31,32
- Smithicyathus* 84,85
- Smithiphyllum* 8,33,49-50
- S. belanskii* 49,51-53,121,122
- presepiments in 51,52,121,122
- septal trabeculae in 52,121
- septotheca in 52
- "Spirifer zone" 15,16,22
- Spongophyllum* 51
- Stratigraphic Distribution, Rugose corals 29
- "striatula zone" 15,17
- Strombodes* 31,32
- S. alpenense* 29
- S. marginatus* 30,31,32,33
- S. knotti* 29
- Strophonellouides* 17
- Stumm, E. 28
- Sulcorphyllum* 84
- Systematic Paleontology 24

<i>Tabulophyllum</i>	8,10,19, 33-34	fine monacanth trabeculae in	34,40,41,43,45,47,48,108,
<i>T. buccinum</i>	47-48 ,118		111,114,117,118
<i>T. curtem</i>	45-46 ,49,100,116,117	peripheral sag of tabulae in	33,35,36,37,38,39,40,
<i>T. densum</i>	46		42,43,110,112
<i>T. ehlersi</i>	35-36 ,37,100,106	presepiments in	33,34,35,36,37,38,40,41,42,44,46,47,119
<i>T. ellipticum</i>	36, 37-38 ,108	septal dilation in	38,40,42,46
<i>T. erraticum</i>	35	septotheca in	34,37,40,41,45,48,115,118
<i>T. exiguum</i>	39	talons in	33,34,36
<i>T. expansum</i>	43-44 ,46,114	talons	33,34,36
<i>T. gorskyi</i>	34	<i>Tarphyphyllum</i>	8,33, 49
<i>T. levorsoni</i>	46-47 ,117,118	<i>T. besti</i>	49
<i>T. longiseptum</i>	45	<i>T. cylindricum</i>	49-50,119,120
<i>T. longum</i>	34, 39-41 ,110,111,112	amplexoid septa in	49
<i>T. mcconnelli</i>	38,39,45	presepiments in	49
<i>T. magnum</i>	41-43 ,46,112,113,114	septal trabeculae in	49
<i>T. manifestum</i>	37	septotheca in	49,50
<i>T. maria</i>	34	trabecular fans	57,70,71,74,85,87,91,137,156
<i>T. mutabile</i>	44-45 ,100,115,116	<i>Trapezophyllum</i>	8,71, 84 ,88,151
<i>T. ovinum</i>	45	<i>T. elegantulum</i>	84
<i>T. ponderosum</i>	38-39 ,109	epithecal wall in	84
<i>T. rectum</i>	33, 34-35 ,36,37,45,100,105,106	ladder-like dissepiments in	84,151
<i>T. regulare</i>	35	Treatise on Invertebrate Paleontology	24,25,53,57,72
<i>T. robustum</i>	39,109	<i>Trigonella</i>	86
<i>T. rotundum</i>	35, 36-37 ,45,107,108	tripartite dissepimentarium	87,88,89,90,154
<i>T. silvaticum</i>	37		
<i>T. traversensis</i>	34,48		
<i>T. zonatum</i>	38,43	Webster, C.L.	8,27
amplexoid septa in	33,36,39,40,42,43,44,47,115,119	Winnebago River	14,15
axial boss in	34,39,42,43		
bilateral symmetry in	34,41,42,44	<i>Zaphrentis solida</i>	53,54,56

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